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Factors affecting the dispersal of coarse fish

Science Report – SC030215

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This report is the result of research commissioned and funded by the Environment Agency's Science Programme.

Published by:

Environment Agency, Rio House, Waterside Drive,
Aztec West, Almondsbury, Bristol, BS32 4UD
Tel: 01454 624400 Fax: 01454 624409
www.environment-agency.gov.uk

ISBN: 978-1-84432-933-5

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Dissemination Status:

Released to all regions
Publicly available

Keywords:

Flood, flow, floodplain, backwater, 0+ fish, stocking, stranding, river rehabilitation, DIDSON, tagging.

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Science Project Number:

SC030215

Product Code:

SCHO0808BOMD-E-P

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Steve Killeen

Head of Science

Executive summary

Habitats for fish in lowland rivers in England and Wales have been extensively modified for flow regulation purposes, including milling, navigation, land drainage and flood prevention. These modifications have degraded fish habitats and restricted the ability of fish to move between them, leading to changes in fish communities. These fish habitats will require mitigation and restoration in order to meet environmental objectives, notably the Good Ecological Status required under the European Commission's Water Framework Directive. Legislation also requires that new schemes avoid adverse effects on biota, including fish. However, our understanding of the factors causing these changes and how best to rehabilitate rivers remains poor. In addition, future challenges, notably climate change and the consequent changes in flow and temperature regimes, may exacerbate these problems.

Stocking of fish is one possible approach to rehabilitating fisheries, particularly after pollution events. However, the dispersal of stocked fish and how this dispersal relates to the physical habitat in the river is poorly understood. This project investigated the patterns of movement of stocked fish before, during and after flow events, in relation to physical habitat, temperature and season, and in comparison with wild fish.

Rehabilitating the physical environment in rivers is another measure advocated for restoring Good Ecological Status. Such rehabilitation requires an understanding of the responses of wild fish populations to floods and high flows. This project describes patterns of lateral and longitudinal movement and the utilisation of various habitats by fish in relation to flow, temperature and season. It also examines losses of fish as a result of their becoming stranded in floodplains following overtopping of floodbanks and the subsequent isolation.

Field studies were conducted on three English rivers: the River Ouse in Yorkshire; the River Trent near Nottingham; and the River Roding, a small tributary of the Thames in Essex. These field studies employed a variety of techniques, including some new technologies. There was therefore a need to demonstrate that the effects of these techniques on fish mortality and behaviour would not significantly influence the results. Trials of tagging methods on small coarse fish were thus undertaken under controlled conditions.

Both the benefits and the harmful consequences of high flows and floods for fish have been widely reported in the scientific literature. However, much of this work has been undertaken on large continental river systems with distinct seasonal flow regimes, and this is also the case with many documented lowland river rehabilitation projects. The aseasonal nature of the flow and flooding characteristics of UK rivers may present different challenges, which this study addresses.

On the Yorkshire Ouse, vast numbers of under-yearling coarse fish were found in temporary floodplain water-bodies following summer floods. Many fish became stranded in waterbodies created by over-topping of floodbanks, being unable to return to the main channel as floodwaters subsided. These young fish were mainly eurytopic species such as roach and bleak, but also included rheophilic species such as chub and dace. Very few fish were found in these habitats during the larger and more frequent winter floods. In summer and winter, backwaters also held large numbers of young fish and thus were also vital habitats for their survival.

Studies of the utilisation of man-made floodplain water bodies on the River Trent and a marina on the Yorkshire Ouse by adult and juvenile fish demonstrated that such water bodies are extensively used by a wide range of coarse fish species. The overall diversity of fish species using these water bodies was enhanced by the fact that they had varying degrees of connectivity to the main river channel according to flow stage.

The predicted effects of climate change on the frequency and magnitude of floods needs to be accounted for when designing and managing man-made waterbodies to ensure the optimum frequency and timing of connections to the river.

Studies conducted in controlled conditions showed that tagging and marking techniques for small coarse fish, employing full- and half-duplex PIT (Passive Internal Transponder) tags, had negligible effects on the survival of hatchery chub and roach and only limited and temporary impacts on their growth. The survival and growth of dace after PIT tagging was poorer, perhaps because of their smaller initial body size.

Studies of the movements of hatchery-reared and wild coarse fish on the River Roding demonstrated good survival of stocked fish: up to 70% of the fish remained after a five-month winter period with numerous high flow events. Movements of both wild and stocked fish were highly correlated with both flow and temperature, but varied between years. Generally, newly-stocked fish moved greater distances than wild fish and these movements were less clearly linked to the locations of favourable habitat. The movements diminished over time, suggesting an initial post-stocking exploratory phase followed by increasing site fidelity. This exploratory phase may bring greater danger of predation and displacement, and may explain the poor persistence of stocked fish observed in other studies.

Further research is required on a number of aspects in order to confirm the details of these findings. The DIDSON methodology described in Chapter 5 shows particular promise for future studies of fish behaviour in relation to physical structures.

This project has demonstrated the links between flows and habitat in lowland rivers and both the lateral and longitudinal movements of coarse fish. It also makes a number of key recommendations for future research and for management action to support Good Ecological Status in English and Welsh lowland rivers.

The design of Flood Risk Management schemes, and habitat restoration and mitigation schemes should incorporate the provision of lateral and longitudinal connectivity between different fish habitats relevant to the species present and local conditions, along the following lines.

- Fish require shelter areas during periods of high flow, especially during summer when the swimming capabilities of small juveniles are limited. Wherever possible, flood levees should be set back as far as possible from the main river to allow connectivity between the river and the floodplain. Where high flow velocities result in fish being displaced over levees, outlet channels should be designed to allow water to drain back into the river smoothly as the floods recede, so that the fish can return to the river. Alternatively, permanent water bodies should be provided in the floodplain.
- Backwater areas are valuable for fish survival in high flows and should be constructed in channelised rivers as part of rehabilitation.
- Man-made floodplain waterbodies with variable connectivity to the main river channel at different discharge stages should be constructed where anthropogenic activities have reduced floodplain habitats.

Natural flow regimes and longitudinal connectivity should be protected and restored.

Restocking programmes can produce good results if account is taken of the availability of suitable habitats and the ability of stocked fish to move between them.

Acknowledgements

The authors would like to thank Dr Jonathan Harvey, Dr Richard Noble, Darren Rollins, Ryan Taylor, David Hunter, Andrea Lalley, Oliver O'Malley, Vasilis Louca, Dave Sayer, Dave Bolland and Laura Wigley for their assistance in data collection. The authors would also like to thank: Barry Byatt, Michael Lee, Neil Winter and other Environment Agency staff for their assistance in data collection; Jon Hateley for providing DIDSON technical support; and Alan Henshaw, Richard Pitman and the other Calverton fish farm staff, who provided, fed and ensured the welfare of the hatchery-reared cyprinids. We are grateful to all landowners for permission to access the rivers.

Contents

Science at the Environment Agency	iii	
Executive summary	iv	
Acknowledgements	vi	
1	General introduction	1
2	Effects of floods on fish	4
2.1	Introduction	4
2.2	Flood concepts	5
2.3	Floods in upland streams	6
2.4	Floods in lowland rivers	10
2.5	Anthropogenic impacts on floods and floodplains	16
2.6	Rehabilitation of flow regimes and floodplains	18
2.7	Conclusions	21
3	Effects of floods on 0+ cyprinid fishes in a constrained lowland river: evidence for backwater and floodplain rehabilitation	22
3.1	Introduction	22
3.2	Materials and methods	23
3.3	Results	27
3.4	Discussion	31
4	Rehabilitation of lowland river-floodplain ecosystems: the importance of variable connectivity between man-made floodplain waterbodies and the River Trent	36
4.1	Introduction	36
4.2	Materials and methods	37
4.3	Results	42
4.4	Discussion	52
5	Imaging fish activity at a lowland river-backwater connection during elevated flow	55
5.1	Introduction	55
5.2	Materials and methods	56
5.3	Results	60
5.4	Discussion	66
6	Evaluation of visible implant elastomer marking and passive integrated transponder tagging protocols for juvenile cyprinid fishes	68
6.1	Introduction	68

6.2	Materials and methods	69
6.3	Results	72
6.4	Discussion	80
6.5	Conclusions and field study recommendations	83
7	Dispersal of stocked cyprinids in a small English river: comparison to wild fish using a multi-method approach	84
7.1	Introduction	84
7.2	Methods	85
7.3	Results	94
7.4	Discussion	103
7.5	Conclusions	108
8	General discussion	110
8.1	Introduction	110
8.2	Conclusions and recommendations	112
	References	116
	List of abbreviations	
	Glossary	

Tables

Table 3.1	Details of sites surveyed for 0+ fishes in the Yorkshire Ouse river (R), backwaters (B) and floodplains (F), including substratum, key aquatic macrophytes and number of times sampled (<i>n</i>)	26
Table 3.2	Frequency of occurrence and relative abundance of 0+ fish captured from the Yorkshire Ouse river (R), backwater (B) and floodplain (F)	28
Table 3.3	Comparison of bleak, chub and roach lengths (mean \pm CI, mm) between main river sites pre-flood and backwater sites during particular flood events	32
Table 3.4	Comparison of bleak, chub and roach lengths (mean \pm CI, mm) between main river sites pre-flood and floodplain sites during the August 2004 flood event	32
Table 3.5	Comparison of fish lengths (mean \pm CI, mm) before and after particular winter flood events (growth assumed to be zero)	34
Table 4.1	Details of sites surveyed for 0+ fishes in the River Trent (R) and floodplain waterbodies (F), including river width (<i>W</i> , m), floodplain waterbody area (<i>A</i> , ha), maximum depth (Max. <i>D</i> , m), dimensions of connectivity channel (<i>W</i> = width, <i>D</i> = depth and <i>L</i> = length, m) or river level rise required for connection (m), connectivity rank (see text for details), substratum and key aquatic macrophytes	40
Table 4.2	Relative abundance of 0+ fish captured from five main river sites (R1–R5) and ten floodplain waterbodies (F1–F10) on the River Trent	43
Table 4.3	Shannon-Wiener diversity index (<i>H'</i>), species richness and Pielou's measure of evenness (<i>J</i>) for all samples from five main river sites (R1–R5) and 10 floodplain waterbodies (F1–F10), and beta diversity (βW) between floodplain waterbodies and local river sampling sites on the River Trent	49
Table 5.1	Mean density (fish $m^{-2} \pm$ SD (%)) at start of each minute processed (<i>n</i> , no. of fish (%)) during day and night sampling periods for all length classes (cm)	62
Table 5.2	Mean (\pm SD (%)) number of fish moving towards the marina per minute during day and night sampling periods for all length classes (cm)	63
Table 5.3	Mean (\pm SD, (%)) number of fish moving away from the marina per minute, during day and night sampling periods for all length classes (cm)	64
Table 6.1	Summary of treatment, species of fish, initial sizes (mm, g) and ratio (%) of PIT tag weight to initial fish mass for each treatment	70
Table 6.2	Survival (% (<i>n</i> , no. of fish)), length (mean \pm SD, mm), mass (mean \pm SD, g), SGR and mark site condition for small chub treatments and control at 29 days, 89 days and 182 days post marking	74
Table 6.3	Survival (% (<i>n</i> , no. of fish)), length (mean \pm SD, mm), mass (mean \pm SD, g), SGR and mark site condition for large chub treatments and control at 29 days, 89 days and 182 days post marking	75
Table 6.4	Survival (% (<i>n</i> , no. of fish)), length (mean \pm SD, mm), mass (mean \pm SD, g), SGR and mark site condition for roach treatments and control at 29 days, 89 days and 182 days post marking	76
Table 6.5	Survival (% (<i>n</i> , no. of fish)), length (mean \pm SD, mm), mass (mean \pm SD, g), SGR and mark site condition for dace treatments and control at 29 days, 89 days and 182 days post marking	77
Table 7.1	Summary of electric fishing surveys for tagging wild fish, including the date sampled, number of sites fished, total length of river fished (m), mean site length (m \pm SD) and the number of fish (all species) tagged	87
Table 7.2	Number (<i>n</i>), length (mean \pm SD (range), mm), mass (mean \pm SD (range), g) and ratio (%) of tag weight of wild and stocked chub	88
Table 7.3	Number (<i>n</i>), length (mean \pm SD (range), mm), mass (mean \pm SD (range), g) and ratio (%) of PIT tag weight of wild and stocked dace	88
Table 7.4	Number (<i>n</i>), length (mean \pm SD (range), mm), mass (mean \pm SD (range), g) and ratio (%) of PIT tag weight of wild and stocked roach	89
Table 7.5	Total population (<i>n</i> \pm SE) and probability of capture (<i>P</i> \pm SE) for chub, dace and roach as determined by the Maximum Likelihood Methods (Carle and Strub 1978) for the three sites sampled quantitatively	90
Table 7.6	PIT antenna operational details, downstream, upstream and milling fish movements recorded and missed, and the proportion of movements missed during 2005–06 sampling	92
Table 7.7	PIT antenna operational details, downstream, upstream and milling fish movements recorded and missed, and the proportion of movements missed during 2006–07 sampling	93
Table 7.8	Number of chub, dace and roach tagged (<i>n</i>) during each sampling occasion and the proportion recaptured (% (<i>n</i>)) in March 2007	96

Figures

Figure 2.1	Various parameters of a flood hydrograph with biological significance (from Welcomme and Halls 2004)	5
Figure 2.2	Geomorphic features of river-floodplain systems (modified from Ward 1998a)	11
Figure 2.3	A conceptual model depicting how floodplain waterbodies exhibit high spatial heterogeneity during the dry phase and progressively reduced spatial heterogeneity during the flood pulse (modified from Ward and Tockner 2001)	12
Figure 2.4	Diversity patterns of different biota along the transect of floodplain connectivity in the River Danube, Austria (modified from Tockner <i>et al.</i> 1998)	12
Figure 2.5	Schematic presentation of main habitat requirements of six fish guilds (modified after Schiemer and Waidbacher 1992, from Schiemer <i>et al.</i> 2004)	14
Figure 2.6	The diversity of habitat in natural and regulated riverine landscapes as a function of the relationship between rejuvenation and terrestrialisation processes (modified from Ward and Tockner 2001)	17
Figure 3.1	Yorkshire Ouse catchment map showing river, backwater and floodplain sampling locations	24
Figure 3.3	Number (a) and percent abundance (b) of rheophilic, eurytopic and limnophilic species captured from the Yorkshire Ouse river (R), backwater (B) and floodplain (F)	29
Figure 3.4	Temporal variations in the density (fish m ⁻²) of 0+ fishes (all species combined) at eight main river sites on the Yorkshire Ouse	30
Figure 3.5	Comparative length-frequency distributions of chub catches from the river (top) and backwater/floodplain (bottom) when (a) similar median fish length but significantly different distribution (Aug 2004), (b) significantly different mean fish length but similar distribution (Oct 2004) and (c) significantly different mean fish length and distribution (Dec 2006)	33
Figure 4.1	A map of England showing the location of the River Trent catchment, and a more detailed catchment map showing sampling sites (site codes are the same as in Table 4.1)	38
Figure 4.2	Mean daily discharge (m ³ s ⁻¹) in the River Trent at Holme Pierrepont in 2006, compared with the long-term daily mean (thin line)	39
Figure 4.3	Number (a) and percent abundance (b) of rheophilic, eurytopic and limnophilic species captured from five main river sites (R1–R5) and ten floodplain waterbodies (F1–F10) on the River Trent	45
Figure 4.4	Costello plots demonstrating 0+ fish community structure at five main river sites on the River Trent	46
Figure 4.5	Costello plots demonstrating 0+ fish community structure at 10 floodplain waterbodies on the River Trent	47
Figure 4.6	Similarity (a) of 0+ fish species composition between five main River Trent (R) and 10 floodplain waterbodies (F) of variable connectivity (b)	48
Figure 4.7	Temporal variations in the density (fish m ⁻²) of 0+ fishes (all species combined) at five main river sites on the River Trent	50
Figure 4.8	Temporal variations in the density (fish m ⁻²) of 0+ fishes (all species combined) at 10 floodplain sites on the River Trent	51
Figure 5.1	Yorkshire Ouse catchment map and Naburn Marina sampling location	56
Figure 5.2	Mean daily discharge (m ³ s ⁻¹ , complete line) in the Yorkshire Ouse at Skelton from (a) August 2005 to August 2006, and (b) during sampling period (13–16 February 2006) and with river level (m, dashed line)	57
Figure 5.3	Example of a DIDSON image, showing three fish (approximately 20cm, 45cm and 50cm long) between 5.5m and 6.5m from the DIDSON transponder	59
Figure 5.4	(a) Fish density (fish m ⁻²) and movements (per minute) (b) towards and (c) away from the marina throughout the study period	61
Figure 5.5	Box plots (10th, 25th, 50th, 75th and 90th percentiles and symbols = outliers) for (a) fish density (fish in sampled area; 4.9m ²) and movements (per minute) (b) towards and (c) away from the marina throughout the study period	65
Figure 6.1	VIE retention (%) in head and fins of chub, roach and dace with time (days)	73
Figure 6.2	Mass frequency of initial size (g) at tagging for 23mm PIT-tagged dace, highlighting fish that died	78
Figure 6.3	Mean length (mm) of chub, dace and roach at time (days) after tagging for control (□), 23mm PIT with adhesive closure (■) and 23mm PIT without closure (Δ)	79
Figure 7.1	(a) Range per day tracked and (b) distance moved per day tracked of chub in the different treatment groups (wild 2005, wild 2006 and stocked 2006)	95
Figure 7.2	Daily distance moved by wild chub, dace and roach (05–06 and 06–07) and stocked chub and roach (06–07), as revealed by mark-recapture, PIT antenna records and a combination of both techniques	98
Figure 7.3	Range of dispersal (mark-recapture) (m) of PIT-tagged wild (a) chub, (b) dace and (c) roach from October 2005 – March 2006 and October 2006 – March 2007	99
Figure 7.4	Stocking locations (fine dashed line: S1, ■; S2, □; and S3, ■) and recapture distribution (batch frequency (%)) of (a) chub and (b) roach	100
Figure 7.5	(a) Flow (m ³ s ⁻¹) and temperature (°C) compared with the daily detections (proportion of fish known to be alive (% day ⁻¹)) of (b) wild chub, (c) wild dace and (d) wild roach during 2005–06 and 2006–07 sampling periods	102
Figure 7.6	(a) Flow (m ³ /s) and temperature (°C) compared with the daily detections (proportion of fish known to be alive that were detected (% day ⁻¹)) of (b) stocked chub and (c) stocked roach during 2006–07 sampling period	104

1 General introduction

Globally, freshwater fishery managers, including the Environment Agency in England and Wales, are faced with a number of impacts that can compromise fish populations. Principle challenges include pollution, flow regulation, habitat fragmentation by weirs and dams, channelisation and habitat degradation (see Cowx 2002), whilst the future also includes the threat of climate change. For example, many lowland rivers have been subject to channelisation and artificial levee construction, reducing rivers to single-thread channels and isolating them from their floodplains (Ward and Stanford 1995a; Cowx and Welcomme 1998). Flow stabilisation and reduced floodplain habitat have also negatively affected fish species highly adapted to periodic inundation for spawning (Kwak 1988; Trexler 1995; Baras and Lucas 2001; Grift *et al.* 2001a, 2003) and nursery (Gehrke *et al.* 1995, 1999; Modde *et al.* 2001; Grift *et al.* 2003).

Such modifications can also have damaging consequences for fishes during floods and high flow events. These can include: increasing the severity of conditions in the main channel (Lusk *et al.* 1998; Poff *et al.* 2006); preventing fish from using floodplain habitats for refuge (Ross and Baker 1983; Kwak 1988); and stranding fish when artificial levees are 'over-topped'. Ultimately, human modifications to river-floodplain ecosystems culminate in reductions in fish abundance and species diversity, and a high number of endangered fish taxa (for example, Ward 1998a; Galat *et al.* 1998; Jungwirth 1998).

The main strategies for addressing these issues and conserving freshwater fish are river habitat improvement and rehabilitation, establishing environmental flows and stock enhancement. River rehabilitation (Cowx and Welcomme 1998) activities to minimise the potential impacts of river engineering are driven in Europe by the Water Framework Directive (WFD; 2000/60/EEC). Protecting biodiversity is driven by the Habitats Directive 92/43/EEC, as well as globally by Agenda 21 of the Rio Convention and the Convention of Biological Diversity. Establishing and enforcing environmental flows (Tharme 2003; Cowx *et al.* 2004) to mitigate activities that alter hydrological regimes are also integral to national (Catchment Abstraction Management System), European (WFD) and global (International Water Management Institute) initiatives.

Stock enhancement (Cowx 1994, 1998) for conservation purposes should only be conducted after the factors limiting stock recovery have been removed or ameliorated (for example, improving water quality or habitat rehabilitation), after which it is likely to accrue long-term benefits. In England and Wales, this compensatory action is based on stocking in excess of two million fish from the Environment Agency fish production facilities, plus millions more from fish farms and fisheries. However, the persistence of cyprinids introduced into some rivers appears to be low (Barnard *et al.* 2002; Aprahamian *et al.* 2004) and there are doubts about the efficiency of the majority of stocking actions.

Integral to the above rehabilitation and recovery programmes is the underlying relationship between fish dispersal and flows, especially high flows. Furthermore, floods are predicted to increase in frequency and magnitude as a result of climate change (IPCC 2002), with a likely associated impact on fish populations. Thus, detailed knowledge and understanding of riverine fish movements is crucial for the effective management and conservation of fish populations. However, there is still a paucity of information about the spatial behaviour and ecology of wild and stocked cyprinids in floodplain rivers. For example, little is known about:

- the importance of man-made floodplain water bodies for juvenile fish (in terms of their significance as spawning and nursery habitats);

- the habitats used by juvenile fish before, during (refuge) and after flood events;
- the amount of fish lost after becoming stranded on historical floodplain areas following flooding events that over-top flood protection structures;
- the lateral movements of adult and sub-adult fish between the main river and floodplain water bodies during winter months and under the influence of elevated flows;
- the short and long-term movements and fate of stocked fish under the influence of environmental variables, especially flow.

Gaps in current knowledge are partly due to juvenile fishes not receiving due attention. But they are also partially attributable to the experimental difficulties of: 1) capturing and identifying the early development stages of fish in the first year of life; 2) observing the movement of adult fish in turbid, lowland rivers; and 3) determining the behaviour of individual sub-adult fish. However, recent advances in capturing and identifying fish larvae (Pinder 2001), sonar equipment (Moursund *et al.* 2003), and tagging and monitoring technology (Lucas and Baras 2000; Zydlewski *et al.* 2001; Gibbons and Andrews 2004) have allowed some of these difficulties to be overcome.

The overall aim of this study was to examine the factors influencing the lateral and longitudinal distribution and movement of juvenile and adult (wild and stocked) cyprinid fishes in lowland rivers and to ascertain the influence of elevated flows on these respective communities. All this was done with a view to conserving and restoring fish stocks by employing effective management measures. To this end, the study was divided into key topics, which are addressed in Chapters 2 to 7. Specific objectives and hypotheses are provided at the start of each chapter.

Chapter 2 reviews the current literature documenting the effects and importance of flood events on species dynamics and fish populations over a river's entire course. This review is conducted with reference to key concepts and principles, longitudinal and lateral connectivity, anthropogenic alterations to the flood pulse and the necessity of rehabilitation programmes.

Chapter 3 investigates the effects of high flow events on the structure and dynamics of the 0+ fish population in the River Ouse (Yorkshire), with particular emphasis on the timing of flooding, the use of refuges (backwaters) during flood events and the stranding of fish behind levees after flood waters recede.

Chapter 4 compares 0+ fish populations in the River Trent and numerous man-made floodplain waterbodies with varying degrees of connectivity. There is particular emphasis upon species composition, community structures, size structure and spawning strategies of the fish populations.

Chapter 5 investigates the winter-time movements of adult fish between the River Ouse and a connected marina using a high-definition imaging sonar, with particular emphasis on diel variations in activity and the effects of elevated flow.

Chapter 6 investigates methods for long-term marking of juvenile cyprinids, with particular emphasis on retention, mortality and growth rates.

Chapter 7 investigates the movement and habitat use of both wild and stocked sub-adult cyprinids in a small river system, with particular emphasis on the influence of temperature and flow, including flood events.

Chapter 8 summarises the information documented in Chapters 3 to 7 in the context of the literature review in Chapter 2. It also summarises management implications and provides recommendations for further study.

The information in this report is intended to guide the management of river fisheries in terms of flood defence initiatives and water resources development. It should also help improve the enhancement and conservation of fish in the future, when problems such as urban development and climate change will affect the functioning of rivers. Specifically, the outputs will inform the future design of river rehabilitation activities and flood alleviation schemes, in order to minimise the potential impacts and maximise the environmental benefits. This study also identifies approaches for maximising the success of future stock enhancement activities.

2 Effects of floods on fish

2.1 Introduction

River ecosystems provide a wealth of goods and services for society, including attenuation and removal of flood waters, water purification, production of fish and other foods and marketable goods, power, recreation and amenity. Similarly, from an ecological perspective, river ecosystems provide high levels of biodiversity, including aquatic flora, and invertebrate and fish fauna that are highly valued by society.

Floods occur when a river exceeds its bank full level. Severe floods may have long-lasting effects on human populations, via their effect on man-made structures and disruption to way of life and commerce. As a result, societies commonly refer to floods as 'disasters' (Haeuber and Michener 1998). However, from an ecological perspective floods in general should not be considered as 'disasters', but as an integral part of the hydrological regime and a beneficial natural disturbance that is essential for maintaining a biologically diverse and productive ecosystem (Bayley 1995; Naiman and Décamps 1997).

Despite the importance of floods to natural ecosystems, many rivers have been subjected to channelisation and artificial levee construction, reducing rivers to single-thread channels and isolating them from their floodplains (Ward and Stanford 1995a; Cowx and Welcomme 1998). This has an impact on the UK's obligations under the WFD to improve the status of fish populations in degraded rivers, because achieving Good Ecological Status may require reconnecting lowland rivers to their floodplains. In addition, the frequency and magnitude of floods are predicted to increase under the influence of climate change (IPCC 2002), with consequences for riverine ecosystem function, biodiversity and productivity (Gibson *et al.* 2005).

Land-use changes may prove to be a greater risk to riverine fishes than projected climate change, but the combined effect of both factors will further alter the functioning of ecosystems and may lead to local species extinction (Peterson and Kwak 1999; Gibson *et al.* 2005). Consequently, there is a need for a greater understanding of the effects of floods on fish and of the ecological implications of anthropogenic alterations to the flood pulse in 'flood-dependent' ecosystems (Bayley 1995; Sparks 1995). This knowledge will assist future attempts to manage, protect and rehabilitate river ecosystems whilst maintaining the requirement to protect property and assets from flooding (minimising human impacts whilst maximising the environmental benefits of floods).

The aim of this review is to uncover the relationships between fish and floods in rivers and the linkages with fish life history strategies, behaviour, assemblage structure and production. More specifically, the objectives are to: 1) summarise the concepts and principles associated with floods; 2) consider how floods shape stream fish communities, especially in constrained upland reaches; 3) outline the importance of floods, floodplains and floodplain connectivity in lowland rivers; 4) discuss anthropogenic impacts on floods and floodplains; and 5) review current attempts to rehabilitate flow regimes and floodplains, thus increasing ecosystem biodiversity and improving the status of fish populations in degraded rivers.

2.2 Flood concepts

Welcomme and Halls (2004) described the hydrological regime of a flood as a curve with several measurable characteristics (Figure 2.1). Ecologically-important components of the flow regime are the amplitude, frequency, seasonal timing, predictability, duration and rate of change of flow conditions (Poff *et al.* 1997; Bunn and Arthington 2002). Every river system has an individual, typical annual hydrological regime, which varies with climate, location, geology, topography and vegetation cover (Van der Nat *et al.* 2003; Cowx *et al.* 2004).

Winemiller (2004) classified rivers globally based on their annual hydrology. These classifications are: temperate with aseasonal (seemingly random) flood pulses; temperate with seasonal flood pulses; and tropical with seasonal flood pulses. However, this gross classification misses many of the subtleties of local river systems, as determined by local geology, geomorphology, and weather variability (Cowx *et al.* 2004).

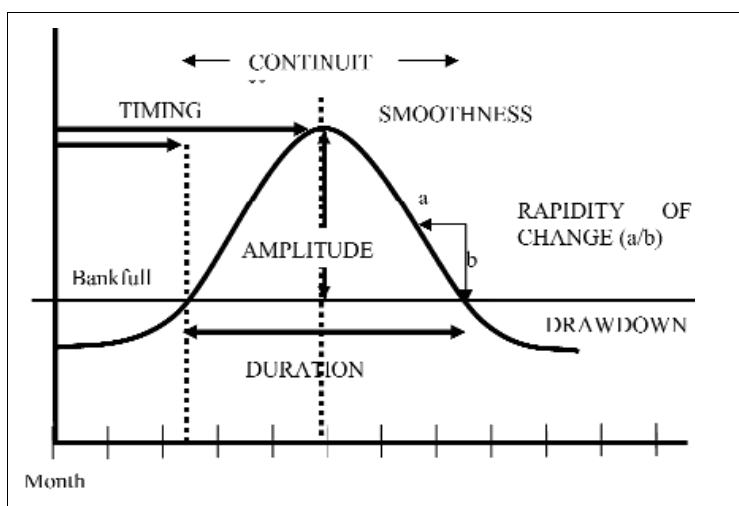


Figure 2.1 Various parameters of a flood hydrograph with biological significance (from Welcomme and Halls 2004)

Over the past 30 years, the development of hydrologic concepts has led to a more detailed understanding and knowledge of riverine ecosystem function and structure, and fish assemblage patterns in response to floods. Building on much earlier concepts of longitudinal zonation (for example, Huet 1949), the River Continuum Concept (RCC; Vannote *et al.* 1980) describes a continuously changing abiotic gradient from headwaters to river mouth, structuring the channel biota. However, floods and floodplain dynamics were not considered until a later version of the RCC (Sedell *et al.* 1989).

Similarly, the serial discontinuity concept (Ward and Stanford 1983) recognised the importance of zonal structure along a water course but ignored floodplain dynamics until Ward and Stanford (1995b) developed their extended serial discontinuity concept (ESDC). The ESDC describes the relative strength of longitudinal, vertical and lateral interactions within a catchment. It revealed that longitudinal (river/river or river/tributaries) pathways are most important in constrained headwaters, vertical (river bed/aquifer) interactions reach their maximum importance in the braided middle course and that lateral connectivity plays a major role in alluvial floodplain (river bed/floodplains) rivers.

The above concepts largely consider longitudinal processes within a catchment, but the Flood Pulse Concept (FPC; Junk *et al.* 1989) states that the lateral connection between the river channel and the connected floodplain during periodic inundation is the major variable driving ecological processes in large tropical and temperate river-floodplain systems (Junk *et al.* 1989; Bayley 1991; Tockner *et al.* 2000b). Junk and Wantzen (2004) have provided a summary of how the FPC has been modified, extended and restricted by several authors as knowledge of both rivers and floodplains has increased considerably. This has come about through studies on the effects of hydrology and hydrochemistry, climate, paleoclimate, biogeography, biodiversity, landscape ecology, and wetland restoration and floodplain management in different latitudes and continents.

Although the FPC is widely accepted and applied by most river ecologists, many consider the theory to have its limitations. For example, the Riverine Productivity Model (RPM; Thorp and Delong 1994) describes the role of autochthonous (indigenous) production in the river channel, but also recognises the importance of the riparian zone and lateral connections. Despite this, Walker *et al.* (1995) stated that riverine models are inadequate to describe the functioning of a river-floodplain ecosystem. Ultimately, a combination of the RCC, the FPC and the RPM might provide a better representation of the energy flow in large rivers (Dettmers *et al.* 2001).

Further to these concepts, it is necessary to consider floods as an essential environmental disturbance occurring along river corridors (Junk *et al.* 1989; Puckridge *et al.* 1998; Swanson *et al.* 1998; Arscott *et al.* 2002), influencing system structure and function (Resh *et al.* 1988; Townsend 1989; Poff 1997; Lake 2000). Sousa (1984) defined a disturbance as 'discrete, punctuated killing, displacement, or damaging of one or more individuals (or colonies) that directly or indirectly creates an opportunity for new individuals (or colonies) to become established'. Alternatively, White and Pickett (1985) concluded that a disturbance could be 'any relative discrete event in time that disrupts ecosystem, community, or population structure and changes resources, substrate availability, or the physical environment'.

Although both definitions state that a disturbance is a discrete event that can be measured by ecological response, the White and Pickett (1985) definition is employed as a working definition in this review because it refers to systems and communities much more generally. Disturbance size, intensity, frequency and predictability determine the community response (Connell and Keough 1985; Poff 1992). The intermediate-disturbance hypothesis predicts that species richness will be highest in communities that experience intermediate levels of disturbance (Connell 1978). Thus rivers with an intermediate (and predictable) level of flooding are expected to provide high diversity. This is because the flooding resets environmental conditions, interrupts community succession and causes increased habitat heterogeneity for many species with different environmental requirements.

2.3 Floods in upland streams

Over evolutionary time, hydrological disturbances (floods) exert primary selective pressure for adaptive processes and thereby influence organism evolution (Stanford *et al.* 1996; Richter *et al.* 1997). Arndt *et al.* (2002) suggested that disturbances of a normal magnitude for the environment are an important part of the natural selection process. As a result, individual fish species have different resistances to flooding based on variations in their life history, behaviour during floods and morphology. Following a flood, the community structure and ecological response is determined by its resistance and resilience (recovery) (Connell and Sousa 1983). Reice *et al.* (1990) suggested that fish populations inhabiting unstable stream environments may be in a constant state of recovery from disturbance.

2.3.1 Fish life history adaptations to the hydrological regime in upland streams

Fish have evolved life history strategies to survive floods based on seasonal timing and predictability, synchronising a life history stage to long-term flow regime dynamics (Poff and Allan 1995). Life history adaptations increase recruitment success by increasing the survival of vulnerable life stages (such as eggs, larvae and juveniles) (Seegrist and Gard 1972). For example, salmonids excavate egg nests deep enough to reduce flood scour to a tolerable level (Montgomery *et al.* 1996; DeVries 1997). The early life stages of some diadromous fish inhabit the marine or estuarine environment in order to avoid exposure to floods (McDowall 1976). Timing spawning so that fry emergence coincides with seasonal periods of low flood probability appears to be an optimal strategy (Heggberget 1988; Montgomery *et al.* 1999; Seegrist and Gard 1972; Erman *et al.* 1988; Hauer *et al.* 1997; Fausch *et al.* 2001).

Conversely, flood events can also be used as cues for spawning and for gaining access to areas of spawning habitat that may not be available at low flows (John 1963; Banks 1969; Alabaster 1970; Nesler *et al.* 1988; Matheney and Rabeni 1995; Naesje *et al.* 1995; Katano and Hakoyama 1997; Swanberg 1997; David and Closs 2002; Ladle 2002). This is particularly the case in intermittent rivers, where elevated flows increase longitudinal connectivity and allow many species to access upstream areas suitable for reproduction and juvenile production (Franssen *et al.* 2006). Furthermore, floods 'flush' silted gravels, thereby improving the spawning substrate and the survival rate of eggs and gravel-related larval life stages (Reiser *et al.* 1989; Wood and Armitage 1997; Milhouse 1998). Indeed, cleaning gravels is an essential service provided by floods to help maintain the integrity of river substrate for successful fish reproduction.

2.3.2 Fish behaviour during floods

Behavioural adaptations to floods are most necessary in the less predictable environments found in upland streams, allowing the fish to respond directly to individual floods to avoid mortality, physical damage or displacement. During a flood, the creation or existence of refugia and disturbance patches influences organism survival and recolonisation potential (Townsend 1989). Pearsons *et al.* (1992) reported that fish populations were more stable in physically complex habitats that provide increased availability of flow refugia. Juvenile and adult fish utilise various low-flow refugia: stream banks and riparian vegetation (Harrell 1978; Matthews *et al.* 1996; Jowett and Richardson 1994; Matheney and Rabeni 1995; Lusk *et al.* 1998; Harvey *et al.* 1999; Brown *et al.* 2001; Lojkásek *et al.* 2005; Gillette *et al.* 2006); rocky shorelines (Deegan *et al.* 1999; Valdez *et al.* 2001); large deep pools with low-velocity areas (Brown *et al.* 2001; David and Closs 2002); in-stream interstitial spaces behind rocks, boulders and woody debris (Tschaplinski and Hartman 1983; Cunjak and Power 1986; Hill and Grossman 1987; Hegggenes 1988; Hegggenes and Traaen 1988; McMahan and Hartman 1989; Fausch and Bramblett 1991; Nickelson *et al.* 1992; Lobón-Cerviá 1996; Kennedy and Vinyard 1997; Harvey *et al.* 1999; White and Harvey 2001); and off-channel areas (Tschaplinski and Hartman 1983; Brown and Hartman 1988; Allouche *et al.* 1999; Bell *et al.* 2001). Ruetz and Jennings (2000) reported that larval robust redhorse (*Moxostoma robustum* (Cope)) may use the boundary layer as a refuge during laboratory swimming tests. Since this layer is approximately 1cm deep, it is also available to a wide variety of other small fish species and early lifecycle stages. Under high-discharge conditions, fish are often attracted to areas of low flow because they are energetically less demanding than maintaining a position in faster water, thus avoiding displacement, physical damage and/or mortality.

2.3.3 Morphological advantages of different fish species during floods

Despite the fact that many studies have considered how the morphological features of fish affect hydrodynamic performance (review in Fish and Lauder 2006), the influence of body morphology on structuring fish communities in freshwaters with differing hydraulic regimes has been somewhat overlooked. While classical texts (such as Lowe-McConnell 1987) describe convergent trends in morphology among species from similar habitats in widely separated ecoregions, only a few studies have been carried out on the value of these attributes to flood-resistant species. Adams *et al.* (2003) speculated that North American cyprinids use oral grasping during energetically demanding flows, such as floods. Gerstner (2007) found that the suckermouth catfish (*Hypostomus plecostomus* (L.)) uses its oral suction disk to improve station-holding performance, but concluded that the use of other morphological features such as the odontodes (dermal teeth) and fin spines may be equally important. Eel-like fishes (syngnathids, calamoichthyis and mastacembalids) are able to survive floods by weaving themselves among stones or aquatic vegetation (R.L. Welcomme, personal communication).

The hydraulic basis of position-holding using paired pectoral fins close to the river bed has been established for many species, including for salmonids (Arnold *et al.* 1991), cyprinids (Facey and Grossman 1990), acipenserids (Adams *et al.* 1999) and cottids (Webb 1989). Tew *et al.* (2002) considered the persistence of a gobiid (*Rhinogobius nantaiensis* (Aonuma and Chen)) before and after a typhoon to be the result of its depressed head and modified pelvic fins, which allow it to hold firmly on to bedrock. However, Webb *et al.* (1996) suggested that, rather than the hydrodynamic properties of the body alone, behavioral traits associated with benthic fish are the most important factors determining the distribution of species in current-swept habitats. Similarly, Ward *et al.* (2003) discovered that desert suckers (*Catostomus clarkii* (Baird and Girard)) and bluehead suckers (*Catostomus discobolus discobolus* (Cope)) use their mouths to suck on to the bottom of a swim chamber, whilst speckled dace (*Rhinichthys osculus* (Girard)) positioned their pectoral fins against the bottom. This reduces energetic expenditure and avoids displacement, but Ward *et al.* still concluded that behavioural responses are more important.

Historic studies considered the nuchal humps (hump behind the head) of benthic species such as the razorback sucker (*Xyrauchen texanus* (Abbott)) and humpback chub (*Gila cypha* (Miller)) to have evolved in order to generate downward force in fast flowing rivers (La Rivers 1962; Miller 1946 cited Portz and Tyus 2004). However, based on evidence from experiments, Portz and Tyus (2004) argued that in two Colorado River fish these large humps are a result of convergent evolution prompted by predation.

2.3.4 Flood-associated mortality

Although fish have evolved life histories, and behavioural and morphological adaptations to avoid and survive high flow events, floods can still cause mortality of juveniles and adults. The effects of high flow events on juvenile fish are directly related to the timing and predictability of floods and the timing of reproduction and fish size (high flow events are most likely to have a major impact on fish if they occur immediately after spawning). Jensen and Johnsen (1999) suggested that moderate flows at a particularly sensitive life stage may cause higher mortality than considerably higher flows at less sensitive stages. For example, high flow events can fill interstitial spaces with silt, preventing alevin (fish larvae) emergence (Phillips *et al.* 1975) or scour salmonid redds and thereby kill incubating embryos (Elwood and Waters 1969;

Seegrist and Gard 1972; Erman *et al.* 1988; Lapointe *et al.* 2000; Carline and McCullough 2003). Once fish emerge – and as their size increases – susceptibility to displacement and mortality declines (Ottaway and Forrest 1983; Heggenes and Traaen 1988; Jowett and Richardson 1989; Nehring and Anderson 1993; Jensen and Johnsen 1999; Valdez *et al.* 2001; Cattaneo *et al.* 2002), although species-specific differences may occur (Crisp and Hurley 1991; Letcher and Terrick 1998). The importance of temperature on swimming performance and susceptibility to downstream displacement has also been documented (Heggenes and Traaen 1988; Jensen and Johnsen 1999; Ruetz and Jennings 2000).

The effects of floods on adult fish are less severe and more predictable than the effects on younger and smaller fish (John 1964; Seegrist and Gard 1972; Hanson and Waters 1974; Hoopes 1975; Tschaplinski and Hartman 1983; Meffe 1984; Schlosser 1985; Fausch *et al.* 2001). In fact, negligible effects of floods on fish of age 1+ or older have been documented (Elwood and Waters 1969; Hill and Grossman 1987; Matthews *et al.* 1994; Harvey *et al.* 1999; Jensen and Johnsen 1999; Lojkásek *et al.* 2005; Pires *et al.* 2008), mainly because older fish with well-developed swimming abilities are able to actively avoid areas of high velocities. However, floods of extreme magnitude can still cause mortality of adult fish (Allen 1951; Elwood and Waters 1969; Seegrist and Gard 1972; Weng *et al.* 2001), although, as with juveniles, vulnerability to flooding may vary between species (Harrell 1978).

Mortality of adult fish during floods mainly occurs in upland reaches, as flow variability, water velocity and intensity of scour are inversely related to stream size. This means that high flow events are more dramatic in upland reaches. For example, adult fish that inhabit the interstitial spaces of the substratum can be crushed by the transport of bed-material during floods (Erman *et al.* 1988; Lusk *et al.* 1998; Swanson *et al.* 1998; Natsumeda 2003; Lojkásek *et al.* 2005). When landslides combine with floodwaters to produce debris flows (mobile slurry of rocks, soil water, and trees moving downstream at up to 10m s⁻¹; Roghair *et al.* 2002), the effects on stream habitats and fish communities are very severe, potentially causing extreme or complete mortality of all age classes of fish (Lamberti *et al.* 1991; Roghair *et al.* 2002; Sato 2006).

Even when a flood doesn't cause the deaths of large quantities of fish, it may still result in reduced growth rates because of invertebrate washout or mortality (Allen 1951; Elwood and Waters 1969; Jensen and Johnsen 1999), reduced foraging efficiency in sub-optimal habitat (Deegan *et al.* 1999), increased activity costs in fast flows and/or reduced foraging efficiency in turbid flood waters (Arndt *et al.* 2002). In the long term, floods may modify river habitat structure, with cumulative negative effects on fish assemblages. For example, floods can remove the gravel substrates that salmonids and other species use for spawning or reduce cryptic habitat for sculpins (Cottidae) exposing them to greater predation (Pearsons *et al.* 1992).

2.3.5 Stream fish population recovery and recolonization after extreme floods

Species living in environments subject to frequent disturbances have evolved adaptations to their life history, behaviour and morphology. As a consequence, the species have also evolved the ability to recover quickly (Matthews 1986; Dolloff *et al.* 1994). After flood-related mortality, elevated growth rates of both age-0 and adult fish have been reported, caused by increased food, reduced competition and/or decreased agonistic interactions (Elwood and Waters 1969; Lamberti *et al.* 1991; Letcher and Terrick 1998; Swanson *et al.* 1998; Roghair *et al.* 2002). Letcher and Terrick (1998) reported that elevated growth rates altered the direction of a crucial life history trait (parr maturation) in age-0 Atlantic salmon (*Salmo salar* L.), possibly allowing more rapid recovery of salmon populations.

Recovery may be aided by the floods improving the quality of bottom sediments (flushing of silted gravels) for the surviving fish, thus elevating the survival rate of spawned eggs in the following reproduction period (Dolloff *et al.* 1994; Harvey *et al.* 1999; Lojkásek *et al.* 2005). The recovery and recolonisation of stream fish populations can also be partly attributed to larger scale migrations from less affected stream reaches (Pearsons *et al.* 2002; Tew *et al.* 2002), influenced by the vagility or colonising ability of fish species (Fausch and Bramblett 1991).

Floods that combine with landslides and cause debris flows have the most severe effect on fish communities. However, Tew *et al.* (2002) could not detect any major changes in the composition of the cyprinid community 14 months after the debris flows and floods associated with typhoon Herb in Taiwan. Other debris flow studies reported that salmonid populations recovered to higher than pre-flood abundance and density within three to five years (Lamberti *et al.* 1991; Swanson *et al.* 1998; Roghair *et al.* 2002). Additionally, Roghair *et al.* (2002) reported that, following a debris flow, subsequent high-flow events altered the channel morphology and reorganised the stream channel to near-pre-event conditions.

2.4 Floods in lowland rivers

In low gradient rivers, floods are characterised by lateral expansion onto floodplains (Welcomme 1979). Floodplains extend from a river's low-water mark to its high-water mark and are ecotones between terrestrial and aquatic environments (Ward *et al.* 1999). The complex gradient of aquatic and riparian habitats collectively produces high structural diversity (Welcomme 1979; Junk *et al.* 1989; Amoros and Petts 1993). The habitat heterogeneity of floodplain river ecosystems is not only maintained but is often increased by erosional and depositional processes during floods (Moore and Gregory 1988; Reeves *et al.* 1995; Mertes 1997; Schroeder and Savonen 1997; Junk *et al.* 1989, Ward 1997; Salo 1990; Ward *et al.* 2002a, c). For example, fluvial action may create fish habitats through the formation of channels, backwaters, standing water bodies and marshes (Figure 2.2; see Amoros *et al.* 1982 for a functional classification of floodplain water bodies).

During periods of low flow, succession towards terrestrialsation re-shapes habitats over time. Major flood events ('flood pulses' *sensu* Junk *et al.* 1989) rejuvenate parts of the aquatic network, reversing the ongoing reduction of ecological connectivity (Amoros 1991). Even small water level fluctuations ('flow pulses' *sensu* Tockner *et al.* 2000b) can lead to major habitat changes (Van der Nat *et al.* 2003). The balance between rejuvenation (erosive flooding) and terrestrialsation processes sustains a constantly changing pattern of habitats in riverine floodplains (Ward 1998a; Ward and Tockner 2001), each potentially characterised by a distinct fish species assemblage (Copp 1989).

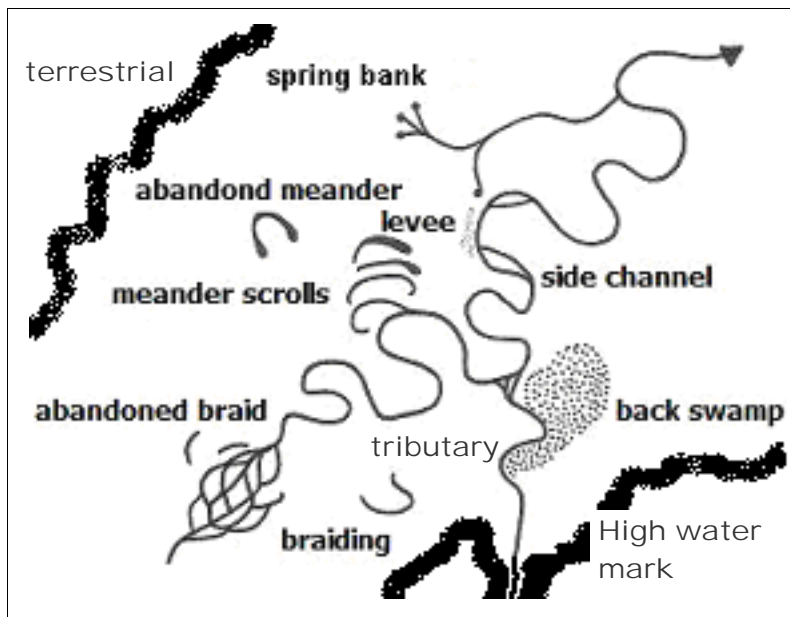


Figure 2.2 Geomorphic features of river-floodplain systems (modified from Ward 1998a)

Floods also play an important role in connecting various landscape patches. During floods, the floodplain shifts from a fragmented and lentic system to a connected and primarily lotic system. This reduces the environmental heterogeneity (Ward 1998a; Tockner *et al.* 2000a, b; Ward and Tockner 2001; Ward *et al.* 2002a, b, c; Thoms *et al.* 2005; see Figure 2.3) and determines the availability of isolated aquatic habitats for fish. Flooding, therefore, enhances hydrological and ecological connectivity between the main river channel and the floodplain. As such, lateral connections are essential for the functioning and integrity of floodplain–river ecosystems (Amoros and Bornette 2002).

The FPC states that the lateral connection between the river channel and the connected floodplain during periodic inundation is the major variable driving ecological processes, biotic interactions and productivity (Junk *et al.* 1989). As such, floodplains of large rivers are among the most productive landscapes on Earth (Tockner and Stanford 2002; Welcomme 2001). Waidbacher (1989) found a positive relationship between hydrological connectivity and the richness of fish species in European aquatic floodplain habitats. Tockner *et al.* (1998) discovered that fish diversity peaked in highly connected habitats on a Danube floodplain, but that other fauna and flora attain different peak species richness along the lateral connectivity gradient (Figure 2.4). Aarts *et al.* (2004) suggested that some RCC predictions could be applied to the transversal floodplain gradient and that the fish guild succession across the transversal floodplain gradient is synonymous with the longitudinal gradient in large rivers.

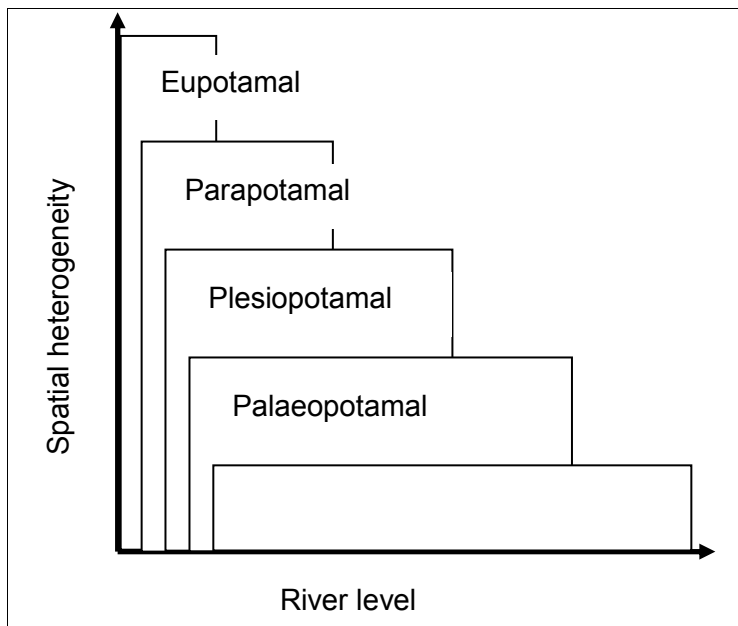


Figure 2.3 A conceptual model depicting how floodplain waterbodies exhibit high spatial heterogeneity during the dry phase and progressively reduced spatial heterogeneity during the flood pulse (modified from Ward and Tockner 2001)

Notes: Eupotamal refers to the main channel or side channels with both upstream and downstream connections to the main channel. Parapotamal refers to side channels with only downstream connections to the main channel. Plesiopotamal refers to a former braided channel that is connected only during high flow. Palaeopotamal refers to former meander loops that are reconnected with the main channel only during floods.

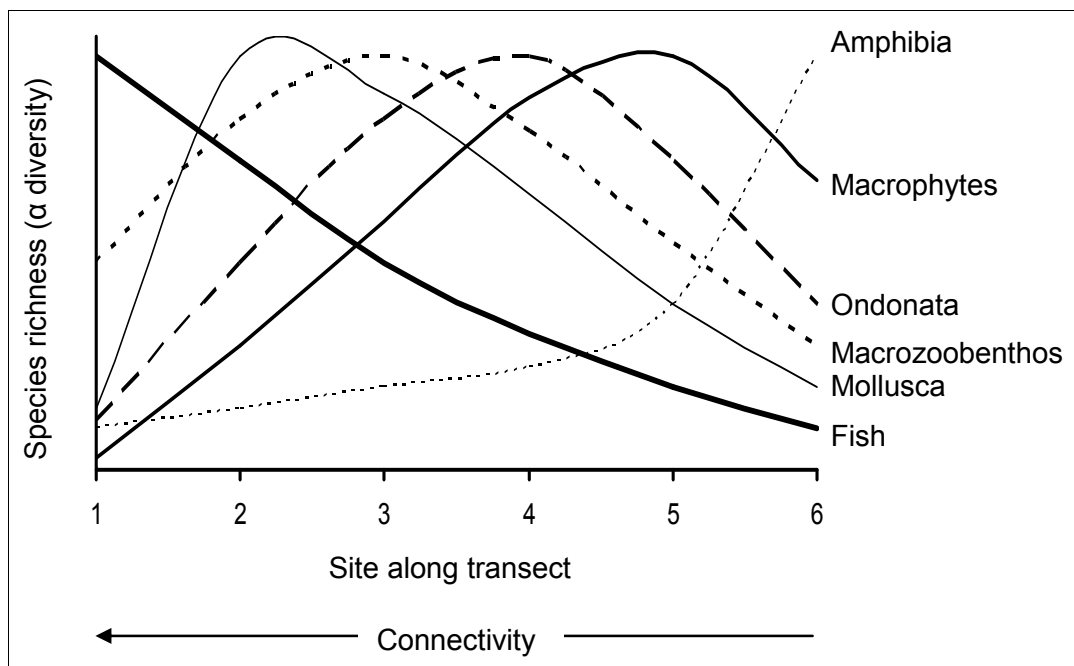


Figure 2.4 Diversity patterns of different biota along the transect of floodplain connectivity in the River Danube, Austria (modified from Tockner *et al.* 1998)

Floodplain habitat heterogeneity and high hydrological connectivity, driven by disturbance (the flood pulse), leads to high levels of productivity and biodiversity (Ward and Stanford 1995a; Ward 1998a; Tockner *et al.* 2000a; Amoros 2002; Robinson *et al.*

2002; Ward *et al.* 2002a, c; Sommer *et al.* 2004b). River-floodplain connectivity during floods allows fish to disperse freely and to take advantage of different floodplain habitats for refuge, spawning, nursery and feeding. After the flood waters recede, the numerous different aquatic habitats at different succession stages contain different fish assemblages, which are further structured by abiotic and biotic interactions. These processes are discussed in more detail in the following section.

2.4.1 Floodplain habitat for fish spawning

In rivers with a seasonal flood pulse (predictable timing), spawning of many fish species coincides with floods, allowing them to exploit relatively predictable habitats and resources on the floodplain (Welcomme 1985; Junk *et al.* 1989). Welcomme and Halls (2001) grouped the reproductive behaviour of tropical river fish into three main categories: fish that spawn in the channel; marginal spawners; and parental care species. For European floodplain rivers, spawning, nursery and adult habitat requirements have led to the formation of six guilds: rhithralic, rheophilic A, rheophilic B, eurytopic, stagnophilic and anadromous species (Schiemer and Waidbacher 1992; Schiemer *et al.* 2004; see Figure 2.5).

Further to this, reproductive strategies can be classified according to where particular species preferentially deposit their eggs (Balon 1975). In natural floodplain systems, diversity in spawning requirements often leads to lateral zonation of fish reproduction, with a sequence of rheophilic-to-eurytopic-to-limnophilic fish species corresponding to a lotic-to-lentic succession of habitat (Copp and Peñáz 1988; Copp 1989; Copp *et al.* 1991, 1994).

In temperate rivers, seasonal changes in temperature and photoperiod influence spawning, which means that the timing of connectivity is crucial (Sparks *et al.* 1990; Junk 1999; Bartosova and Jurajda 2001). In catchments with substantial snow-covered uplands, such as found in mainland Europe (Schiemer *et al.* 2004, Buijse *et al.* 2002, Raat 2001), temperate seasonal floods are caused by elevated temperatures and rainfall leading to melting snow (Winemiller 2004). Floodplains bordering snow-melt rivers possess a temperature advantage, as shallow depths promote early seasonal warming via solar radiation (Modde *et al.* 2001; Jackson 2004).

In rivers with an aseasonal flood pulse (when the flood pulse can be decoupled from the temperature pulse, as in and the UK and Australia), high temperatures trigger spawning during low flows. This led Humphries *et al.* (1999) to propose the 'low flow recruitment hypothesis'. However, Molls (1999) found that adult bream (*Abramis brama* (L.)) develop permanent stocks in oxbow lakes on the River Rhine because of the irregularity of connection, thus giving bream a reproductive advantage over other species. As discussed for fish in upland streams, floods of irregular timing in lowland rivers can be highly damaging. This is particularly the case if high flows occur immediately after spawning, as larvae and juveniles are highly susceptible to displacement and mortality (Harvey 1987; Simonson and Swenson 1990; Mann and Bass 1997; Mion *et al.* 1998; Thieme *et al.* 2001; Nunn *et al.* 2007b).

Further to these key principles, many studies from around the world have reported that adult fish spawning is synchronised with flooding periodicity, in order to ensure larvae develop on the floodplain (Lowe-McConnell 1975; Guillory 1979; Halyk and Balon 1983; Ross and Baker 1983; Tyus 1987; Kwak 1988; Sabo *et al.* 1991; Sabo and Kelso 1991; Peñáz *et al.* 1992; Gehrke 1992; Turner *et al.* 1994; Sparks 1995; Agostinho and Zalewski 1995; Killgore and Baker 1996; Fernandes 1997; Gomes and Agostinho 1997; Poizat and Crivelli 1997; Sommer *et al.* 1997; Winemiller and Jepsen 1998; Sparks *et al.* 1998; Modde *et al.* 2001; Sommer *et al.* 2001a, b; Jurajda *et al.* 2004; Barko *et al.* 2006; Lojkásek *et al.* 2005). Ward *et al.* (1999) emphasised that the

movement of fish to floodplain spawning and nursery areas is crucial for the recruitment and sustainability of fish populations.

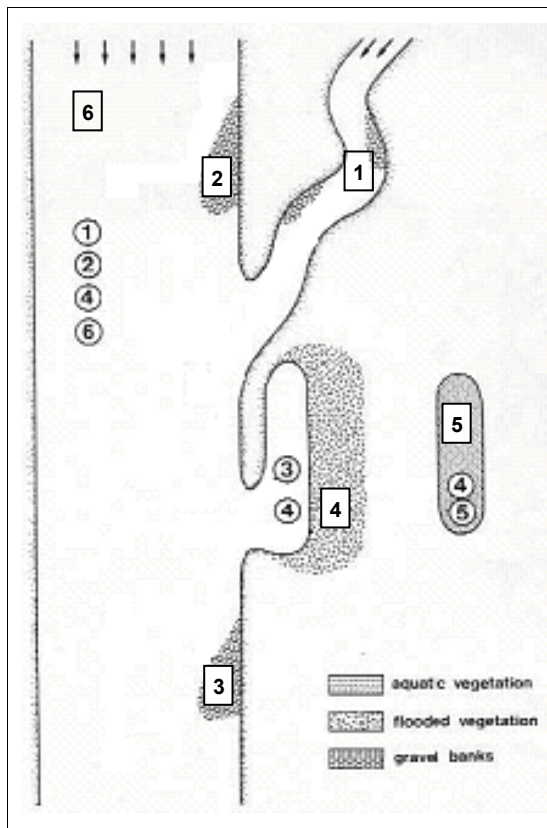


Figure 2.5 Schematic presentation of main habitat requirements of six fish guilds (modified after Schiemer and Waidbacher 1992, from Schiemer *et al.* 2004)

Notes: Circles = preferred habitats of adults; squares = spawning and nursery sites; 1 = rhithralic, 2 = rheophilic A; 3 = rheophilic B; 4 = eurytopic; 5 = stagnophilic; and 6 = anadromous species

2.4.2 Floodplain habitat for fish nursery

The FPC suggests that fish spawning coincides with floodplain inundation because nutrient release stimulates the production of phytoplankton and zooplankton, thus providing abundant food resources for newly hatched larvae (Junk *et al.* 1989) in tropical and temperate rivers (Bayley 1995). Sommer *et al.* (2001a) used bioenergetic modelling to show that the feeding success of young chinook salmon (*Oncorhynchus tshawytscha* (Walbaum)) was greater in the Yolo Bypass floodplain than in the Sacramento River, resulting in higher growth rates. Enhanced macrophyte growth also provides spawning substrate for many species and cover for young fish. Inshore zones (connected secondary channels and oxbow lakes) are of high value as fish nurseries (Griff *et al.* 2001b; Simons *et al.* 2001), because they possess high structure and low flow, and provide significant food production (Schiemer *et al.* 2001).

Thus, inundated floodplain habitats allow young progeny to take advantage of abundant food resources, refuge from velocity and shelter from predators. However, high levels of tannins and decaying plant matter, and the resultant low levels of dissolved oxygen, may severely impact the abundance and diversity of fish larvae (Gehrke *et al.* 1993; Lusk *et al.* 1998; Swales *et al.* 1999; Fontenot *et al.* 2001). In the latter context, Gehrke (1990) demonstrated that golden perch (*Macquaria ambigua*

(Richardson)) larvae may actively avoid inundated floodplain areas if the water quality is unsuitable.

2.4.3 Flood intensity and duration

In rivers with seasonal flood pulses (predictable timing), inundated floodplains provide benefits to both adult and juvenile fish, but these benefits depend on the magnitude and duration of the flood pulse (Junk *et al.* 1989). Welcomme and Halls (2004) reviewed the influence of the hydrological regime on fisheries. They found that floods of greater amplitude increased the area available for spawning sites, as well as increasing the amount of food and shelter, whilst the duration of the flood influenced the time available for fish to grow and shelter from predators.

These principles apply to rivers around the world: large floods of long-term duration increase fish species richness and abundance in both temperate (Jurajda *et al.* 2004; Modde *et al.* 1996) and tropical (Gomes and Agostinho 1997; Agostinho *et al.* 2000) floodplain systems. However, different species respond differently to different types of flood regime (Welcomme and Halls 2004; Welcomme *et al.* 2006). For example, Agostinho and Zalewski (1995) discovered that Brazilian floodplain fish feeding on flooded grasslands and on riparian fruits and leaves were dominant groups in years with large floods. Similarly, Jurajda *et al.* (2004) found that long-term flooding increased the abundance of phytophilous and phytolithophilous species (Balon 1975). They also suggested that flooded vegetation provided food and shelter, leading to increased growth and reduced predation. Floods of short duration or low amplitude have the most detrimental effect when spawning involves nest building and adhesive eggs, because of the risk of desiccation (Humphries *et al.* 1999). The hydrological variability of the flood pulse can therefore have a marked influence on the year class strength of fishes, causing annual variations in species assemblages.

2.4.4 Floodplain habitat for fish refuge during floods

Floodplain connectivity plays an important role in determining the severity of conditions in the main channel during floods (Poff *et al.* 2006). Lojkásek *et al.* (2005) noted that stream ecosystems are less resistant to the destructive effects caused by floods in upper stream sections than in lower ones with developed floodplains. However, as documented for fish in upland streams, the relationship between flood timing and fish size is crucial for fishes in lowland rivers (Harvey 1987; Mann and Bass 1997). In addition, the behavioural adaptations of fish also determine their survival during flood events.

Many studies report the movement of fish onto inundated floodplains (Guillory 1979; Ross and Baker 1983; Kwak 1988; Bell *et al.* 2001). Other studies report migrations into floodplain waterbodies (Sedell *et al.* 1990; Molls and Neumann 1994) for refuge during floods, especially into vegetated and depositional floodplain habitat with negligible velocity (Griff *et al.* 2003; Schiemer *et al.* 2004; Schwartz and Herricks 2005). Humphries *et al.* (2006) hypothesised that slack water refuges provide juvenile fish with energetic advantages, primarily because of the poor swimming capabilities of these fish. If high flows occur at times when metabolic capacity is low (low temperatures), and hence the capability of fish to withstand elevated current velocity is low, the availability of low current refuge areas may be crucial. However, fish can become stranded on the floodplains when flood waters recede (Bain *et al.* 1988; Brown *et al.* 2001; Ortlepp and Murle 2003; Lojkásek *et al.* 2005), or they can take up residence in isolated floodplain waterbodies until they are liberated by a future flood event. In the former case, there is a net loss to recruitment in that period; whether this

affects year class strength depends on the intensity of the stranding and loss of the cohort.

2.4.5 Floodplain water bodies during low flows

As water levels drop, fish either migrate back to the river, providing food for river-resident piscivores (Fernandes 1997), or they are concentrated in isolated floodplain water bodies. In tropical floodplains, 10–70% of fishes are found only in floodplain waterbodies variously connected to the main channel (Welcomme 1985). Lateral differences in the environments of floodplain waterbodies produce differences in species distributions associated with physiological and morphological adaptations between fishes (Dudgeon 2000; Welcomme *et al.* 2006). Welcomme (1985) documented that the assemblage characteristics of fishes reflects the size of floodplain waterbodies, with larger fish inhabiting larger floodplain pools. Abiotic variables such as pH, oxygen, turbidity, depth and macrophyte cover also affect isolated water body fish assemblages in perennial tropical (Rodriguez and Lewis 1997; Tejerina-Garro *et al.* 1998; Suarez *et al.* 2001; Petry *et al.* 2003a, b, c; Hoeinghaus *et al.* 2003; Pouilly and Rodriguez 2004) and temperate floodplains (DeAngelis *et al.* 1997; Grift 2001; Winemiller *et al.* 2000; Feyrer *et al.* 2004). Biotic variables such as predator/prey interaction (Rodriguez and Lewis 1997; Suarez *et al.* 2001) and disease risk (DeAngelis *et al.* 1997; Bartosova *et al.* 1999) are also strong determinants of assemblage composition.

Stochastic floods produce different disturbance and colonisation regimes in perennial rivers, strongly influencing fish species assemblages (Zeug *et al.* 2005). However, similar relationships between assemblage structure and physicochemical characteristics can also occur during isolation (Zeug *et al.* 2005; Arthington *et al.* 2005). Floodplain waterbodies can eventually dry up, resulting in the deaths of all fish present (Lusk *et al.* 1998). Ultimately, abiotic and biotic (predation and competition) controls over fish in floodplain water bodies can cause localised extinctions of species that are unable tolerate the environmental conditions and/or modulate recruitment of juveniles to riverine populations.

2.5 Anthropogenic impacts on floods and floodplains

Many studies document the extent to which regulated rivers deviate from a pristine state (see Cowx 2002). Dynesius and Nilsson (1994) found that dams, reservoirs, inter-basin diversions and irrigation strongly or moderately affected 77% of the flows from the 139 largest rivers in the northern third of the world. In a more recent global overview of large river systems, Nilsson *et al.* (2005) found that over half of the river systems (172 of 292) were affected by dams. Constructing dams for flood control or hydroelectric power generation imposes serial discontinuities (Ward and Stanford 1983, 1995b), alters the natural flow (and flood) regime (*sensu* Poff *et al.* 1997) and can result in dramatic loss of ecological integrity and spatial heterogeneity (Toth *et al.* 1995; Schmidt *et al.* 1998; Molles *et al.* 1998; Jungwirth *et al.* 2000; Schiemer 2000; Snyder *et al.* 2003; Thoms 2003). Altering the river flow regime is considered to be the most detrimental human alteration to freshwater ecosystems (Stanford *et al.* 1996; Poff *et al.* 1997).

Flow regulation, channelisation and artificial levee construction (Ward, 1998a; Amoros and Bornette 2002) reduce rivers to single-thread channels. These rivers have a shortened shoreline length and are isolated from their floodplains and lentic waters (oxbows and pools) (Petts *et al.* 1989; Ward and Stanford 1995a; Neumann *et al.* 1996; Cowx and Welcomme 1998; Tockner and Stanford 2002; Thoms 2003; Schiemer *et al.*

2004). Levees can completely cut off parts of the former floodplains from erosive, scouring flood flow, thus preventing the creation of new floodplain waters. This reduces rejuvenation and accelerates the terrestrialisation of existing water bodies (Tockner and Bretschko 1996; Ward 1998b; see Figure 2.6). Up to 90% of European and North American floodplains are 'cultivated' and therefore functionally extinct (Tockner and Stanford 2002).

Driven by disturbance (the flood pulse), floodplain habitat heterogeneity and high hydrological connectivity leads to high levels of productivity and biodiversity. As such, most human alterations are likely to cause a reduction in biodiversity and productivity in both the main river channel and its accompanying floodplain waterbodies. This is a function of reducing the lateral connectivity, altering successional trajectories and disrupting seasonal water level fluctuations. Thus, in 'flood-dependent' ecosystems the prevention of floods is considered a disturbance (Bayley 1995; Sparks 1995).

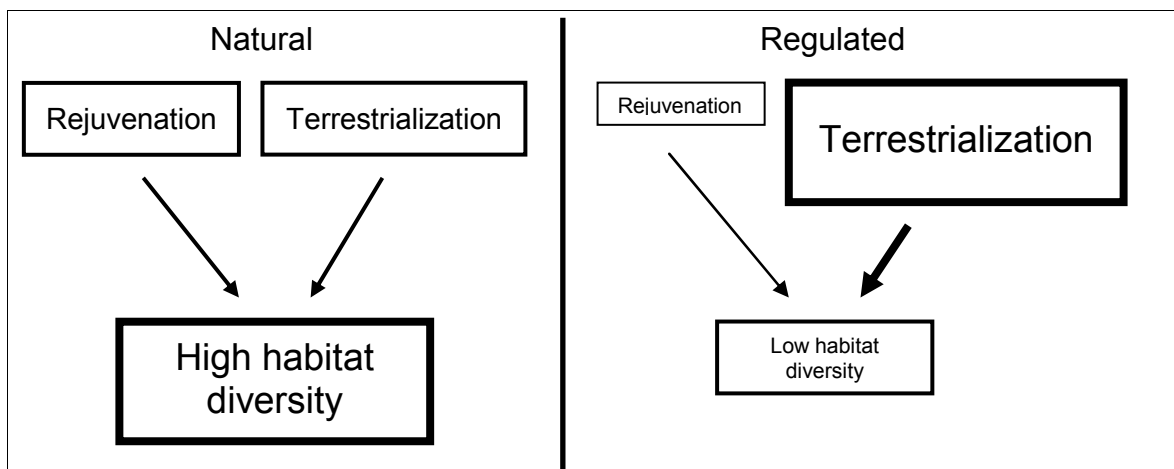


Figure 2.6 The diversity of habitat in natural and regulated riverine landscapes as a function of the relationship between rejuvenation and terrestrialisation processes (modified from Ward and Tockner 2001)

Nilsson *et al.* (2005) stated that human modifications to the hydrologic regime and floodplain connectivity are impacting fish communities globally. Where natural flash floods are regulated by upstream dams, stabilised flows often favour alien fish species, which prey on and compete with native fish (Meffe 1984; Moyle and Light 1996a, b; Reid and Brooks 2000) or are better able to tolerate the harsher conditions in the modified environment. Aarts *et al.* (2004) reported that ecological fish guilds are unevenly affected in heavily regulated rivers, with rheophilic species becoming (very) rare because their lotic habitats have been lost or degraded. However, they also found that the floodplain transversal succession gradient in the fish community resembled that seen in natural rivers, because plesiopotamal and paleopotamal lakes are still present in regulated river-floodplain systems. Flow stabilisation and reduced floodplain habitat have been reported to affect fish species that require periodic inundation for spawning (Kwak 1988; Trexler 1995; Baras and Lucas 2001; Grift *et al.* 2001a, 2003), nursery (Gehrke *et al.* 1995, 1999; Modde *et al.* 2001; Grift *et al.* 2003), flow refuge (Bischoff and Wolter 2001) and food web structure (Power *et al.* 1996).

The loss of floodplain habitat also has a knock-on effect on in-channel species. The absence of flooding in regulated sections of the upper River Paraná in Brazil has had adverse effects on many fish species due to a lack of access to out-of-channel habitat, resulting in increased predation in the channel (Agostinho *et al.* 2001). The composition of the fish fauna in dammed channels changes from a rheophile-dominated

assemblage to eurytopic forms (Schiemer and Waidbacher 1992). Schiemer and Zalewski (1992) suggested that the RCC might be more appropriate than the FPC for describing the functioning of floodplain rivers restricted to channels by levees, based on the dominant role of longitudinal processes. Welcomme *et al.* (2006) proposed using environmental guilds as indicators of fish assemblage responses to hydrological, morphological and functional changes in a river.

It is important to consider the potential for a time lag between abiotic changes and abiotic adjustments, since floodplains respond slowly to anthropogenic impacts (making it is easy to underestimate the extent of degradation). This means that apparent high biodiversity in regulated floodplains may often be a relic of former conditions (Tockner and Stanford 2002). For example, Tockner and Bretschko (1996) suggested that the high invertebrate diversity in former floodplains adjacent to a regulated section of the River Danube in Austria is a transitional state related to the high spatial heterogeneity. Ultimately, however, these former floodplains are succeeding toward terrestrialsation. Additionally, subtle effects of the modifications and schemes may have been, and may remain, undetected (Craig *et al.* 2004).

Ultimately, human modifications to the river-floodplain ecosystem culminate in more fish taxa becoming endangered and a loss of species diversity (Ward 1998a; Galat *et al.* 1998; Jungwirth 1998; Collares-Pereira *et al.* 2002). Robinson *et al.* (2002) suggested that the complex life cycles of many fauna in intact riverine landscapes implies that species loss translates to a loss in the evolutionary trajectories of morphology, physiology, behaviour and complex life cycles. Tockner and Stanford (2002) emphasised the urgent need to preserve floodplain rivers intact and to restore impacted systems to prevent extinctions of species and ecosystem services.

2.6 Rehabilitation of flow regimes and floodplains

Much of the knowledge about the structure and function of river-floodplain landscapes is based on research conducted in the tropics on unregulated rivers (Junk *et al.* 1989). However, it is generally assumed that unchanged temperate rivers function in a comparable way to tropical river-floodplain rivers (Welcomme 1995), although differences in climate can influence some seasonal processes. Brown (2002) stated that if river restoration is to have an ecological, as opposed to 'cosmetic', design, it is necessary to question the natural river-floodplain state and whether it can be recreated. The ecological conditions of rivers before channelisation are poorly known (for example, the Kissimmee River; Trexler 1995), although, with sufficient hydrologic variation, unmodified reaches can remain intact (Sparks *et al.* 1990; Poff *et al.* 1997; Richter *et al.* 1997).

Inadequate data from pristine natural systems can hinder the restoration of river-floodplain systems. Additionally, Hauer and Lorang (2004) asked: 'Can a reasonable amount of natural functionality be restored while also allowing traditional human uses of the river and its floodplains?' This is a particular challenge where re-establishing natural floodplain functioning compromises societal values, property and economic investment. Consequently, restoring aquatic habitats towards pristine conditions can be considered a utopian ideal (Cowx *et al.* 2004). Tockner and Stanford (2002) and Schiemer *et al.* (1999) suggested that restoration projects should serve as large-scale field experiments to provide a better understanding of the dynamics and complexity of riverine floodplains. Hauer and Lorang (2004) suggested that recovery towards a 'normative' condition allows many, if not most, of the historical natural resource uses of rivers to occur within historical ranges of variation. However, this is compromised in large urban areas where such adjustment is not feasible.

Restoration strategies should not focus on a single taxonomic group or species (Sparks 1995; Tockner *et al.* 2000a), because different faunal groups have different environmental requirements. For example, different taxonomic groups peak in performance at different positions along the connectivity gradient (Tockner *et al.* 1998). However, flagship species can highlight key issues and track progress in addressing these issues. For example, nase (*Chondrostoma nasus* (L.)) has become a key conservation species for highlighting the environmental conditions of large European rivers (Schiemer *et al.* 2003).

Conservation plans that target only one species but incorporate habitat protection and improvements can confer wider benefits to ecosystem health and allow a wider diversity of species to flourish (Collares-Pereira and Cowx 2004). Cowx and Welcomme (1998) suggested that the process of rehabilitating rivers for fish should involve reinstating lateral and longitudinal connectivity, recreating habitat diversity and channel morphology, improving flow regimes for fisheries purposes and resolving water quality problems. In many cases, the removal of dams to improve longitudinal connectivity is not possible, while water quality nowadays rarely limits riverine fish populations, certainly in Europe (Van Dijk *et al.* 1995; Cals *et al.* 1998; Nienhuis and Leuven 2001; Raat 2001). Hence, riverscape management and rehabilitation strategies should focus on restoring hydro-geomorphological dynamics to increase spatio-temporal heterogeneity (Amoros and Bornette 2002).

Tockner *et al.* (1998) suggested that restoring the integrity of the hydrograph is the most vital step in restoring rivers. Several studies have attempted to model the environmental flow regimes necessary for protecting or restoring river ecosystems: for example, the RVA (Range of Variability Approach; Richter *et al.* 1997), the DRIFT (Downstream Response to Imposed Flow Transformations) methodology (King *et al.* 2003) and others (Arthington and Pusey 2003; Arthington *et al.* 2003; Richter *et al.* 2003; reviewed in Tharme 2003; Cowx *et al.* 2004). Re-regulating flows by rescheduling dam releases to simulate natural intra- and interannual variation of hydrologic regimes (magnitude, timing, duration, variability and frequency) 'naturalises' regulated rivers (*sensu* Poff *et al.* 1997). The process thus protects native biodiversity and the evolutionary potential of aquatic, riparian and wetland ecosystems (Richter *et al.* 1996, 1997; Stanford *et al.* 1996; Poff *et al.* 1997).

Stanford *et al.* (1996) argued that flows should be re-regulating, so that the river performs most of the geomorphic restoration of floodplain habitats, rather than using heavy equipment to engineer artificial solutions. Bischoff and Wolter (2001) reported that habitat diversity increased in the River Oder in response to a very large flood and suggested that more large floods could enhance fish recovery in this highly regulated system. In the Kissimmee River (Florida, US), restoration of a more natural hydrologic regime has resulted in an increased growth rate for largemouth bass (*Micropterus salmoides* (Lacepède)), which are now reaching their maximum size (Arrington and Jepsen 2001). Many studies have also documented the benefits of dam-release floods for enhancing native fish populations over non-native fish (Meffe and Minckley 1987; Marchetti and Moyle 2001; Valdez *et al.* 2001; Brown and Ford 2002; Schultz *et al.* 2003), primarily because of varying behavioural responses during flood events (Meffe 1984; Ward *et al.* 2003).

Cowx and Gerdeaux (2004) highlighted the necessity of recreating functional habitats for spawning, feeding, nursery (growth) and resting (self-protection), as well as the connectivity between them, in order to improve the ecological functions of the river system (Schiemer *et al.* 1999). As a result, levees should be set back, lowered or removed, while secondary channels should be created and isolated oxbows reconnected (Van Dijk *et al.* 1995; Cals *et al.* 1998; Tockner *et al.* 1998; Simons *et al.* 2001; Lusk *et al.* 2001, 2003). These processes have the capacity to restore floodplains, backwaters and floodplain water bodies, reinstate hydrological connectivity

and increase habitat complexity (Gore and Shields 1995; Stanford *et al.* 1996; Aarts *et al.* 2004). Such restoration or rehabilitation efforts may only be necessary for limited reaches to maintain the fishery and biodiversity – the ‘string of beads principle’ (Cox and Welcomme 1998).

Artificial floodplain ponds (borrow pits excavated during dyke construction) connected to the main channel function as excellent fish spawning, nursery, feeding, winter and shelter habitats, replacing habitat lost during river regulation (Sabo and Kelso 1991; Staas and Neumann 1996). This is especially the case if coupled with controlled flooding of the floodplain habitat (Jurajda *et al.* 2004). Grift *et al.* (2003) observed that fish habitat use in man-made secondary channels (rheophilic fish) and reconnected oxbow lakes (eurytopic fish) was comparable to (semi-)natural floodplains, with different water bodies having complementary values. This finding emphasises that future floodplain rehabilitation should focus on water bodies with diverse habitats.

Simons *et al.* (2001) also concluded that man-made secondary channels can function as a biotope for riverine fish species, including the more demanding rheophilic species. Sommer *et al.* (2002) reported that floodplain restoration improves floodplain connectivity during low flows, with benefits for the reproduction of splittail (*Pogonichthys macrolepidotus* (Ayres)) in dry years. In addition, restoring seasonal hydrology and increasing river floodplain connectivity benefits native fish and reduces the impacts of non-native fish (Gutreuter *et al.* 1999; Sommer *et al.* 2001b; Sommer *et al.* 2004a; Barko *et al.* 2006), although the opposite has also been reported (Scheerer 2002).

Tockner and Stanford (2002) stated that natural uses of floodplains far outweigh the value of human activities that constrain floodplain structure and function. Not only are such statements unrealistic (socio-economic constraints), they also fail to take account of the benefits of floodplain structure and function to humans. Floodplains store huge amounts of water and change the flood pulse from short, devastating peak discharges to lower discharges of longer duration. They are natural flood control structures that can provide human flood protection.

Brenner *et al.* (2003) reported that ecologically-sensitive flood control structures enhanced fish recruitment and diversity along the rivers Rhine and Meuse. In addition, Poff (2002) detailed a successful example of non-structural flood controls managed for wildlife habitat on the Charles River in the US. These controls cost less than 10% of the projected cost of the originally proposed dam and levee project. Since the impact of floods on human habitation are the driving forces in river corridor and floodplain management, there is an urgent need to ensure that soft engineering flood protection methods, which are sensitive to fisheries, are integral to future human flood management strategies. Consequently, ecologists need to play a major role in providing education and leadership regarding the benefits for both humans and biodiversity of natural hydrological regimes and the associated habitat within catchments (Collares-Pereira *et al.* 2002).

2.7 Conclusions

Floods are an essential component of the hydrological regime, influencing riverine ecosystem function and structure and fish assemblage patterns throughout the catchment. In upland streams, floods are hydrological disturbances influencing the evolution of the life history, behaviour and morphology of fish species. Floods of irregular timing and magnitude can cause the deaths of juveniles and adults, but in upland streams fish species have generally evolved the ability to recover quickly.

In more lowland reaches, floods are characterised by lateral expansion onto floodplains, resulting in high levels of habitat heterogeneity that are essential for fish refuge, spawning, nursery and feeding. As reported for upland reaches, floods of irregular timing can cause the deaths of juveniles in temperate aseasonal rivers. However, variations in the magnitude and duration of floods can also have significant influence on species assemblages in seasonal rivers. Anthropogenic alterations to the flow regime and floodplain connectivity can reduce biodiversity and productivity in both the main river channel and its accompanying floodplain waterbodies.

Rehabilitation efforts should reinstate lateral and longitudinal connectivity by restoring a more natural hydrologic regime and recreating functional habitats – recovery towards a ‘normative’ condition – thus providing human flood protection whilst maximising ecological benefits. More specifically, hard engineering flood defences should not seek to constrain and channelise rivers, but should instead link floodplain habitats over a range of flow conditions while simultaneously enhancing localised flood protection.

This will require protecting the remaining free-flowing and natural hydroseral habitats from physical engineering and sensitively reconnecting floodplains on land (often agricultural) adjacent to zones requiring flood defence. By necessity, this strategy precludes wide-scale physical flood protection of human communities on floodplains and thus implies stringent development restriction in floodplain areas. As such, this strategy is likely to require changes in land management and flood defence practices, some of which are already being instituted within England and Wales – for example, *Making space for water* (DEFRA 2005).

3 Effects of floods on 0+ cyprinid fishes in a constrained lowland river: evidence for backwater and floodplain rehabilitation

3.1 Introduction

Connectivity between rivers and their floodplains is essential for the proper functioning and integrity of floodplain ecosystems (Amoros and Bornette 2002). River-floodplain connectivity allows fish to disperse freely and to take advantage of different floodplain habitats for refuge, spawning, nursery and feeding (Chapter 2). However, many rivers have been subject to channelisation and artificial levee construction, reducing them to single-thread channels and isolating them from their floodplains (Ward and Stanford 1995a; Cowx and Welcomme 1998). Reduced floodplain habitat has been reported to affect fish species that require periodic inundation for spawning (Kwak 1988; Trexler 1995; Baras and Lucas 2001; Grift *et al.* 2001a, 2003) and nursery (Gehrke *et al.* 1995, 1999; Modde *et al.* 2001; Grift *et al.* 2003).

Such modifications can also have adverse consequences for fishes during floods and high flow events. This is because of the resultant hazardous conditions (including increased water velocity and bed load transport) in the main channel (Lusk *et al.* 1998; Poff *et al.* 2006). In addition, fish can be prevented from using floodplain habitats for refuge (Ross and Baker 1983; Kwak 1988) and become stranded when artificial levees are 'over-topped'. This is of particular importance to 0+ fishes (fish in their first year of life) because of their poor swimming capabilities (Harvey 1987; Humphries *et al.* 2006).

Furthermore, abiotic factors are increasingly being recognised as an important factor influencing inter-annual variability in the recruitment success of cyprinid fishes (Nunn *et al.* 2007b). However, relatively little is known about the habitat use of age 0+ fishes before, during and after flood events in relation to the timing of those events. This issue is of particular importance, as the frequency and magnitude of floods are predicted to increase under the influence of climate change (IPCC 2002). Additionally, climate change is predicted to interact with existing riverine alterations and further impact ecosystem functioning (Peterson and Kwak 1999; Gibson *et al.* 2005).

The aim of this study was to determine the effect that floods of varying timing and magnitude have on 0+ cyprinids in a constrained lowland river, as well as to assess the significance of these effects and, if necessary, suggest mitigative measures. This was achieved by sampling the 0+ fish populations of the Yorkshire Ouse in: (1) the main river channel on a fortnightly/monthly basis; (2) backwaters during flood events; and (3) areas of water isolated from the main river channel behind levees after flood waters receded. Specifically, the objectives were to compare the community structure, density and size composition of 0+ fish species in the main river with 0+ fish species in backwaters and on floodplains during and after floods.

3.2 Materials and methods

3.2.1 Study area

The Yorkshire Ouse (Figure 3.1) in north-east England is one of the UK's largest single-thread rivers and has been isolated from its floodplain by channelisation and levee construction. The river drains 10,000km² of predominantly rural catchment, and has an average width of 50m and a depth of 3–4m; its water quality is generally good (Neal and Robson 2000). Precipitation run-off from the Pennines often results in elevated river levels and out-of-bank floods, such as happened in August, October and December 2004, March, May and December 2006, and January 2007 (Figure 3.2).

3.2.2 Surveys of 0+ fish

Sampling was carried out at eight river sites, six backwater sites and five floodplain sites (Table 3.1). The river sites were in the margins of the main channel in areas devoid of large woody debris. The water was ≤ 1.5 m deep with a slow velocity, where 0+ fishes tended to aggregate. Populations of 0+ fish at river sites were surveyed in daylight hours at intervals of 14–30 days from April 2004 to February 2007, inclusive. The exception was during June and July 2006 when no sampling was undertaken because of an outbreak of Viral Hemorrhagic Septicaemia (VHS) at a fish farm within the catchment.

Backwaters were areas of slack water sampled during elevated river levels and floods. They consisted of plateaus between the main river channel and the levees (B1, B2 and B3), a 'backed-up' tributary (B4), a slipway between two buildings (B5) and a bay downstream of some large marginal willows (*Salix* spp.) (B6). Four of the floodplain sites flooded via levee over-topping: two (F1 and F2) drained through underground drains; one (F5) drained via a 'flap-gated' ditch but left a substantial area of isolated water; and one (F3) emptied through a sluice with any residual water extracted by pump. The fifth floodplain site (F4) was flooded by a manually-operated sluice (upstream end) and drained through a sluice (downstream end) after river levels receded, with any residual water extracted by pump. After floods, sampling on floodplains began as soon as areas of water became isolated from the main river channel.

All samples were collected using a micromesh seine net (25m long by 3m deep with a 3mm hexagonal mesh) set in a rectangle parallel to the bank by wading. The seine net captured larvae as small as 5mm, although its efficiency was reduced for fish smaller than around 15mm (Cowx *et al.* 2001). Captured fish were identified to species (Pinder 2001), separated into six larval (L1–L6) and one 0+ juvenile (J) developmental step (Copp 1990; Peñáz 2001), and measured for standard length (SL; nearest mm).

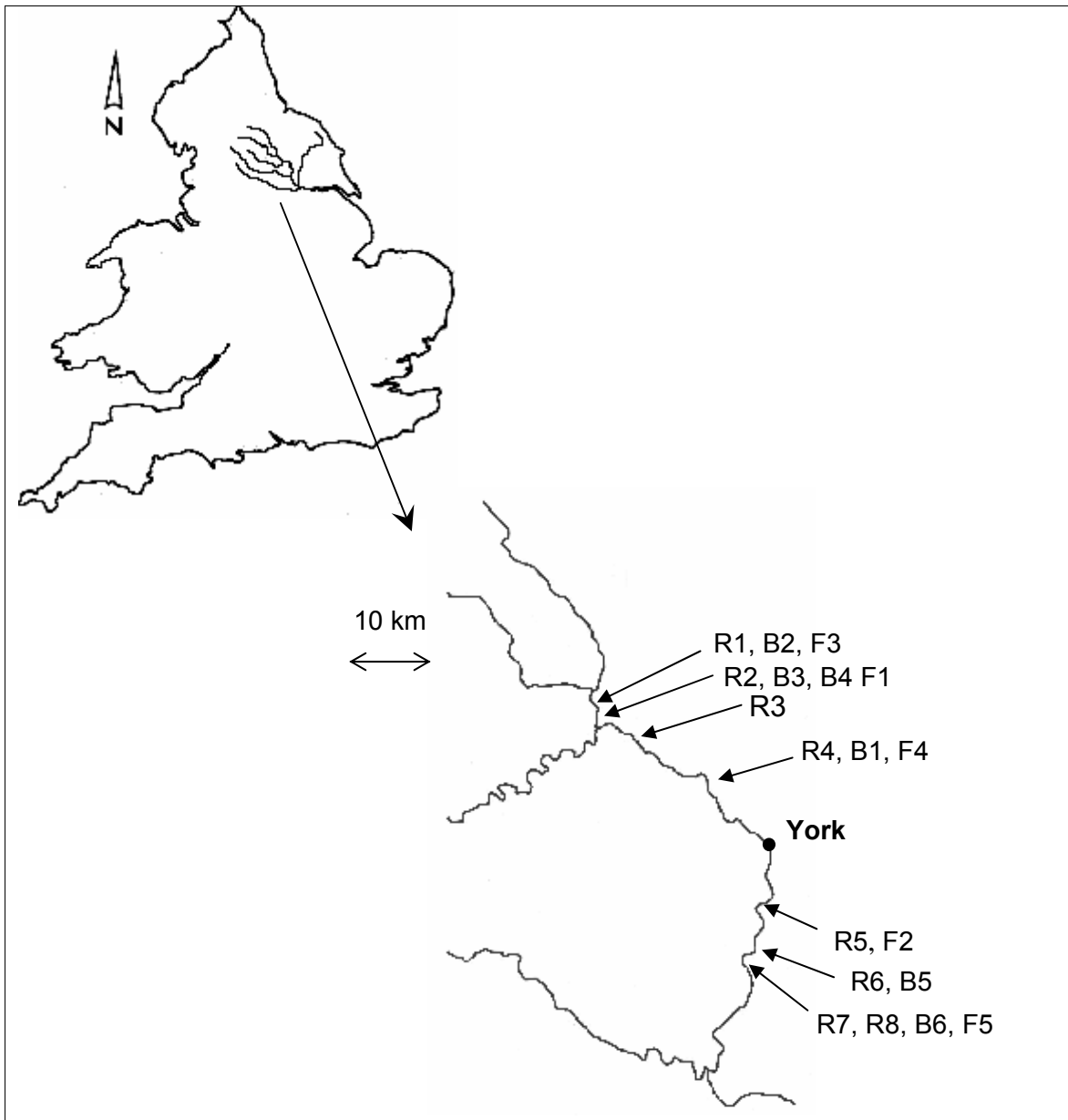


Figure 3.1 Yorkshire Ouse catchment map showing river, backwater and floodplain sampling locations

3.2.3 Data analysis

For each site sampled, we calculated the frequency of occurrence and relative abundance of each fish species from all the surveys (Hynes 1950). We also calculated the Shannon-Wiener diversity index (H'), species richness, Pielou's measure of evenness (J) (Washington 1984) and relative density (fish m^{-2}) of 0+ fishes (all species combined) for each sampling occasion. The frequency of occurrence of a given species was defined as the number of surveys in which the species occurred, expressed as a frequency of the total number of surveys in which fish were captured. The relative abundance of a species was defined as the percentage of total catches (numbers) in all surveys accounted for by the given species.

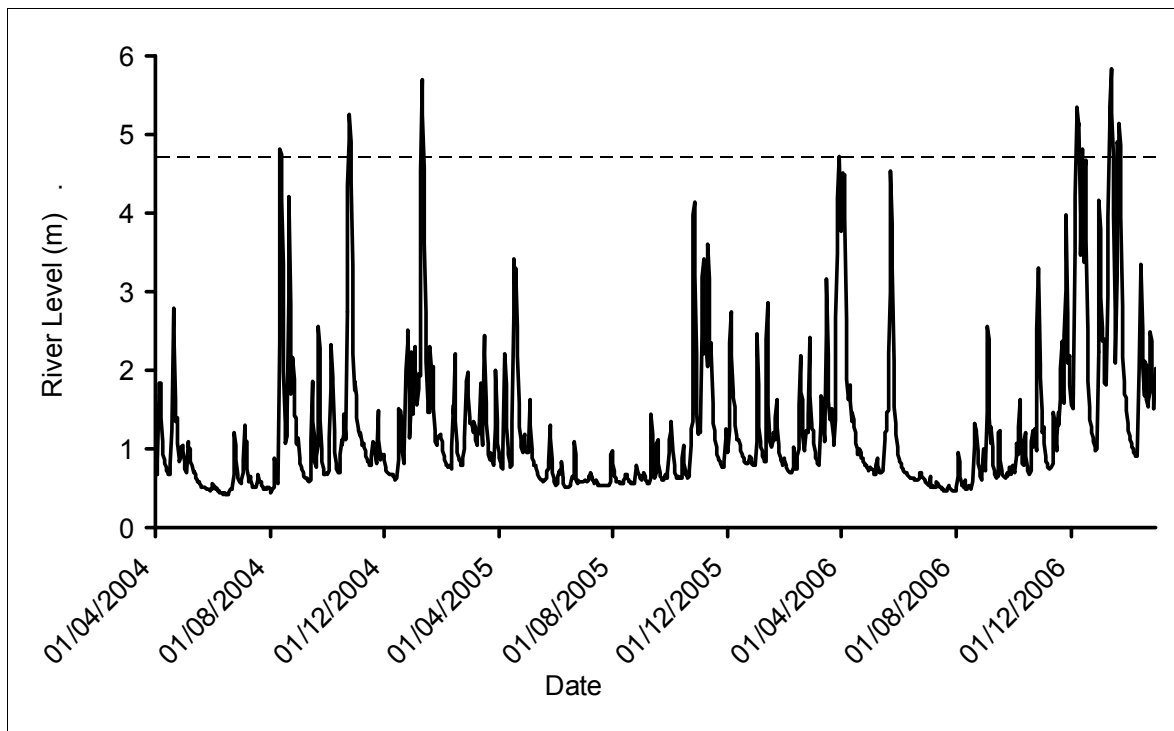


Figure 3.2 Mean daily river level (m) in the Yorkshire Ouse at Skelton from April 2004 to February 2007

Note: --- = river level when 'out-of-bank' floods occur.

Mann-Whitney U-tests were used to test the null hypothesis that the mean, H' , richness, J and density of 0+ fishes for all surveys at each site did not differ significantly between the river and backwater/floodplain sampling units. Mann-Whitney U-tests were used to test the null hypothesis that there was no difference in overall H' and the relative abundance of the main species – bleak (*Alburnus alburnus* (L.)), chub (*Leuciscus cephalus* (L.)), dace (*Leuciscus leuciscus* (L.)), gudgeon (*Gobio gobio* (L.)) and roach (*Rutilus rutilus* (L.)) – in the river at the end of summer in 2005 (no floods during summer) and 2006 (elevated flow period during May; see Figure 3.2).

Mean SL (independent samples t -tests), median SL (Mann-Whitney U -tests, when variances were not equal Levene statistic $P < 0.05$) and length distributions (two-sample Kolmogorov-Smirnov tests) of each fish species in the river before floods were compared with fish in backwaters, on floodplains and in the river after floods. These comparisons tested the null hypotheses that there was no significant difference in 0+ size for fish in the river prior to floods compared with fish in backwaters and stranded on floodplains in the river after the floods, respectively. Comparisons were restricted to backwater and floodplain sites that had adjacent river sites (to avoid potential bias caused by spatial variations in fish size) and to samples with sufficient numbers (>30) of a given species. All statistical analyses were carried out using Statistical Package for Social Sciences (version 14.0) with a significance level $\alpha = 0.05$.

Table 3.1 Details of sites surveyed for 0+ fishes in the Yorkshire Ouse river (R), backwaters (B) and floodplains (F), including substratum, key aquatic macrophytes and number of times sampled (*n*)

Site name	Habitat	Code	Dimensions	Substrate	Key aquatic macrophytes	<i>n</i>
Linton	Main river	R1	River width 50m, max. depth 3–4m, sampling depth 1.2m	Sand/clay	<i>Potamogeton pectinatus</i> L. (little)	31
Newton	Main river	R2	River width 50m, max. depth 3–4m, sampling depth 1.2m	Sand/clay	<i>P. pectinatus</i>	19
Beningbrough	Main river	R3	River width 50m, max. depth 3–4m, sampling depth 1.2m	Sand/clay	<i>P. pectinatus</i>	28
Clifton	Main river	R4	River width 50m, max. depth 3–4m, sampling depth 1.2m	Sand/clay	-	19
Fulford	Main river	R5	River width 50m, max. depth 3–4m, sampling depth 1.2m	Mud/silt	<i>P. pectinatus</i>	30
Naburn	Main river	R6	River width 50m, max. depth 3–4m, sampling depth 1.5m	Sand/clay	-	19
Acaster Malbis	Main river	R7	River width 50m, max. depth 3–4m, sampling depth 1.5m	Concrete	-	31
Naburn weir	Main river	R8	River width 70m, max. depth 3–4m, sampling depth 1.5m	Sand/clay	<i>P. pectinatus</i>	19
Clifton	Backwater	B1	River width 100m, max. depth 9–10m, sampling depth 2m	Grass	-	8
Linton car park	Backwater	B2	River width 150m, max. depth 10–12m, sampling depth 1m	Concrete	-	3
Newton	Backwater	B3	River width 100m, max. depth 9–10m, sampling depth 1m	Grass	-	3
River Kyle	Backwater	B4	River width 30m, max. depth 9–10m, sampling depth up to 10m	Grass	-	2
Naburn	Backwater	B5	River width 100m, max. depth 9–10m, sampling depth 1m	Concrete	-	3
Naburn weir	Backwater	B6	River width 100m, max. depth 10–12m, sampling depth 2–4m	Grass	-	2
Newton Ings	Floodplain	F1	Ings surface area 3ha, drained down sampling area 0.5ha, depth 0.5m	Grass	-	6
Nun Ings	Floodplain	F2	Ings surface area 1ha, drained down sampling area 0.15ha, depth 0.5m	Grass	-	5
Linton Ings	Floodplain	F3	Ings surface area 20ha, drained down sampling area 0.2ha, depth 0.5m	Grass	-	2
Rawcliffe Ings	Floodplain	F4	Ings surface area 20ha, drained down sampling area 0.3ha, depth 0.5m	Grass	-	4
South Ings	Floodplain	F5	Ings surface area 25ha, drained down sampling area 0.5ha, depth 0.5m	Grass	-	1

3.3 Results

3.3.1 Species composition

More than 250,000 specimens of 19 fish species were captured during the study period (Table 3.2). Of these 19 species, all but rudd (*Scardinius erythrophthalmus* (L.)) were captured from the main river; 14 species (>25,000 individuals) were caught from backwaters; and 12 species (>20,000 individuals) were captured on floodplains. Roach, gudgeon, chub and bleak occurred most frequently in the main river and backwater catches. Roach, chub and bleak also occurred most frequently on floodplains, but gudgeon were captured less often on floodplains (Table 3.2).

Median H' was significantly higher in the river surveys during normal flows than in backwaters during floods (Mann Whitney U -test: $Z = -2.160$, $n = 13$, $P = 0.031$), but this was not the case with median richness (Mann Whitney U -test: $Z = -0.154$, $n = 13$, $P = 0.877$). Median H' and richness were significantly higher in the river surveys during normal flows than on floodplains after floods (Mann Whitney U -test: H' : $Z = -2.623$, $n = 13$, $P = 0.009$; richness: $Z = -2.006$, $n = 13$, $P = 0.045$). Median J did not differ significantly between river surveys during normal flows and in backwaters during floods (Mann Whitney U -test: $Z = -0.926$, $n = 13$, $P = 0.355$) or on floodplains (Mann Whitney U -test: $Z = -1.852$, $n = 13$, $P = 0.064$).

Roach (39%), gudgeon (20%), chub (16%) and bleak (14%) were the most abundant fish species in the river, while backwaters and floodplains were dominated by eurytopic species (bleak = 53% and 29%; roach = 25 and 41%, respectively) (Figure 3.3). Chub abundance in backwaters (10%) was similar to in the river, but was higher on the floodplains (26%). Gudgeon were rarely found on floodplains (mean abundance = 0.1%), but accounted for up to 27% of the catches in backwaters (B1), along with some strictly rheophilic species such as barbel (*Barbus barbus* (L.)) and stone loach (*Barbatula barbatula* (L.)) (Table 3.2).

During May 2006, a flood (Figure 3.2) coincided with the period immediately after fish hatching, and larvae of roach (L1–L3; 7.5 ± 0.7 mm), dace (L3–L4; 11.6 ± 0.8 mm), chub (L4; 12.8mm), perch (*Perca fluviatilis* L.) (L2–L6; 13.5 ± 1.5 mm) and minnow (*Phoxinus phoxinus* (L.)) (L2–L3; 8.4 ± 0.4 mm) were all found in the river and backwaters. Unfortunately, an outbreak of VHS prevented post-flood sampling of the floodplains and main river sites until August 2006, rendering immediate investigation of the impacts of the flood on the 0+ fish community impossible. Although there was a flood when the fish were in their larval period, it did not have a significant effect on H' (Mann Whitney U -test: $Z = -1.722$, $n = 18$, $P = 0.085$).

The relative abundances of the main species (Mann Whitney U -tests: bleak: $Z = -0.574$, $n = 18$, $P = 0.566$; chub: $Z = -0.580$, $n = 18$, $P = 0.562$; dace: $Z = -1.820$, $n = 18$, $P = 0.069$; gudgeon: $Z = -0.397$, $n = 18$, $P = 0.691$; roach: $Z = -1.634$, $n = 18$, $P = 0.102$) in August 2006 were similar to those in August 2005, suggesting that the flood had no significant impact upon the species composition of the 0+ fish community.

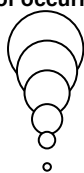
Table 3.2 Frequency of occurrence and relative abundance of 0+ fish captured from the Yorkshire Ouse river (R), backwater (B) and floodplain (F)

Family Species	Vernacular name	Flow pref. ¹	Occurrence			Abundance		
			R	B	F	R	B	F
Balitoridae								
<i>Barbatula barbatula</i> (L.)	Stone loach	Rheo A	○	○	.	○	○	.
Cottidae								
<i>Cottus gobio</i> L.	Bullhead	Rheo A	○	.	.	○	.	.
Cyprinidae								
<i>Barbus barbus</i> (L.)	Barbel	Rheo A	○	○	.	○	○	.
<i>Alburnus alburnus</i> (L.)	Bleak	Eury	○	○	○	○	○	○
<i>Abramis brama</i> (L.)	Bream	Eury	○	○	○	○	○	○
<i>Leuciscus cephalus</i> (L.)	Chub	Rheo A	○	○	○	○	○	○
<i>Leuciscus leuciscus</i> (L.)	Dace	Rheo A	○	○	○	○	○	○
<i>Gobio gobio</i> (L.)	Gudgeon	Rheo B	○	○	○	○	○	○
<i>Phoxinus phoxinus</i> (L.)	Minnow	Rheo A	○	○	○	○	○	○
<i>Rutilus rutilus</i> (L.)	Roach	Eury	○	○	○	○	○	○
<i>Scardinius erythrophthalmus</i> (L.)	Rudd	Limno	.	○	.	.	○	.
<i>Abramis bjoerkna</i> (L.)	Silver bream	Eury	○	.	.	○	.	.
Esocidae								
<i>Esox lucius</i> L.	Pike	Eury	○	○	○	○	○	○
Gasterosteidae								
<i>Gasterosteus aculeatus</i> L.	Three-spined stickleback	Eury	○	○	○	○	○	○
<i>Pungitius pungitius</i> (L.)	Ten-spined stickleback	Limno	○	.	○	○	.	○
Percidae								
<i>Gymnocephalus cernuus</i> (L.)	Ruffe	Eury	○	○	○	○	○	○
<i>Perca fluviatilis</i> L.	Perch	Eury	○	○	○	○	○	○
Pleuronectidae								
<i>Platichthys flesus</i> (L.)	Flounder	Rheo C	○	.	.	○	.	.
Salmonidae								
<i>Thymallus thymallus</i> (L.)	Grayling	Rheo A	○	.	.	○	.	.

Note: 1. Flow preference classification according to Schiemer and Waidbacher (1992) – Rheo A = rheophilic A, Rheo B = rheophilic B, Eury = eurytopic and Limno = limnophilic.

Key (percent frequency of occurrence and abundance)

Dominant (> 75 %)
 Abundant (51-75 %)
 Frequent (26-50 %)
 Occasional (6-25 %)
 Infrequent (1-5 %)
 Rare (< 1 %)
 Not captured



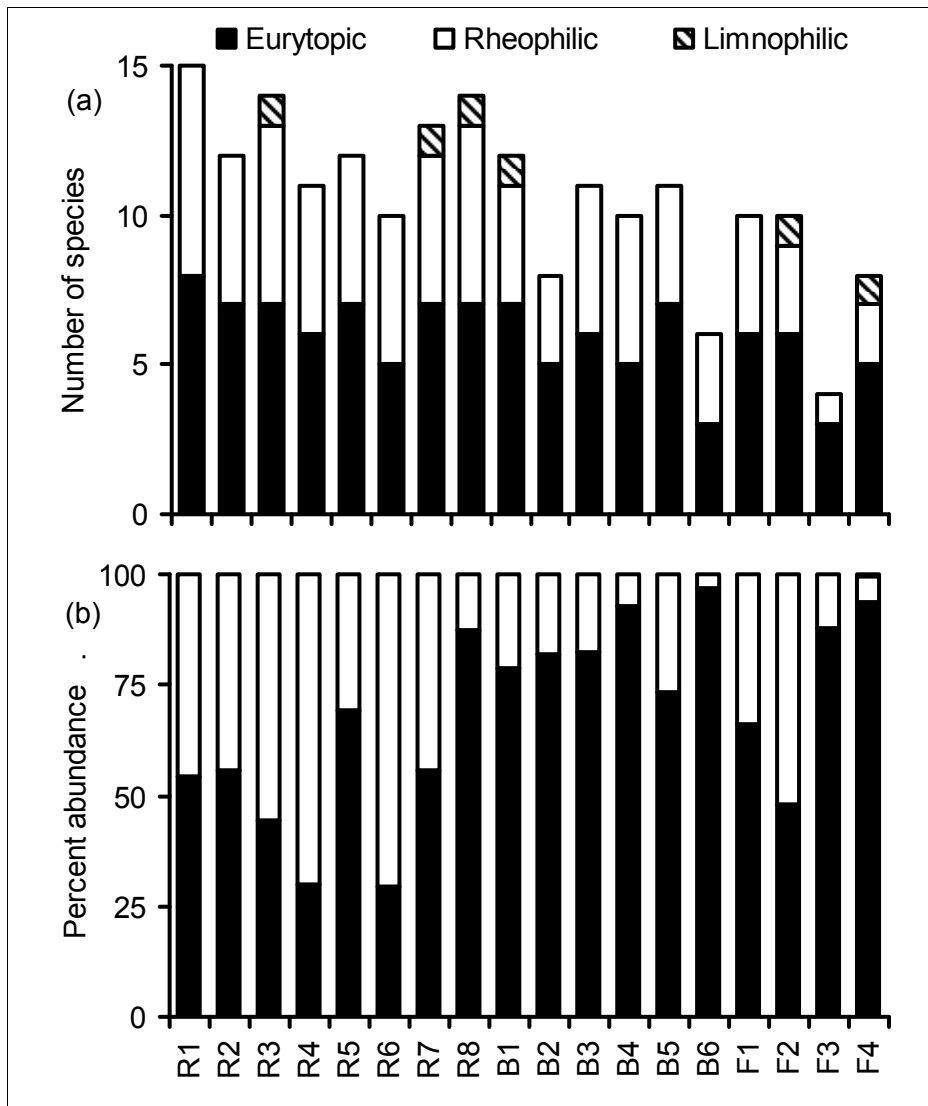


Figure 3.3 Number (a) and percent abundance (b) of rheophilic, eurytopic and limnophilic species captured from the Yorkshire Ouse river (R), backwater (B) and floodplain (F)

Note: Flow preference classification according to Schiemer and Waidbacher (1992).

3.3.2 Density

Overall, the mean density of 0+ fishes captured during routine river sampling (all samples from R1–R8) was 11 ± 40 fish m^{-2} , but substantial spatial and temporal variations occurred (Figure 3.4). At the site level, the highest mean (39 fish m^{-2}) and maximum (455 fish m^{-2}) densities were found at R1, with the lowest mean density at R5 (2 fish m^{-2}). Densities of 0+ fishes were low in May, but increased in June and July. They generally peaked in August, once the majority of species had hatched and grown to a size when they could be effectively captured by the seine net (Figure 3.3). Thereafter, densities declined as the fish dispersed from the nursery areas and as density-dependent and density-independent factors acted upon the 0+ fish populations. Densities of fish in main river sites before and after floods and at the end of each summer were not compared because the temporal variations in density were so large (Figure 3.4).

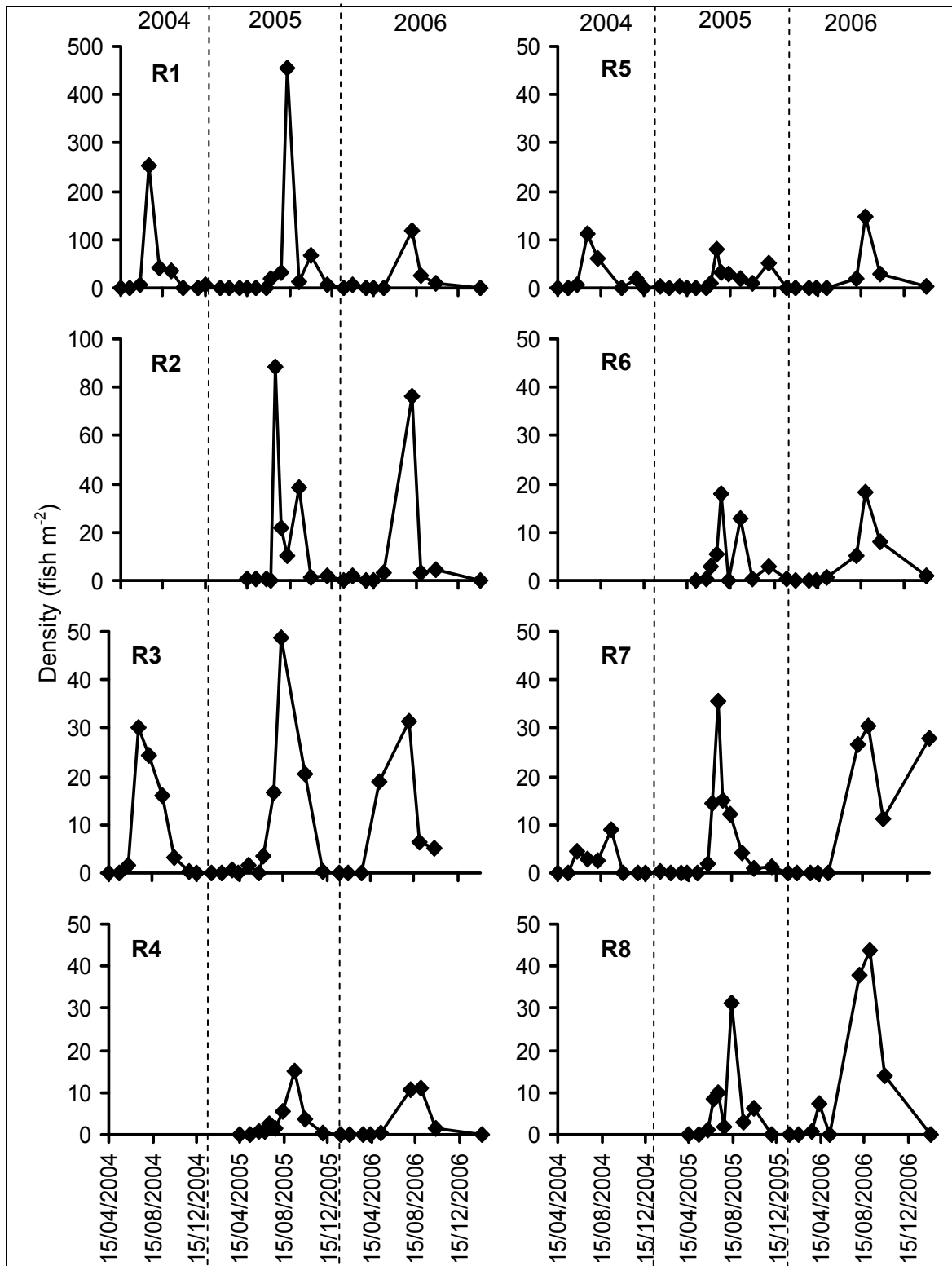


Figure 3.4 Temporal variations in the density (fish m⁻²) of 0+ fishes (all species combined) at eight main river sites on the Yorkshire Ouse

Notes: Site codes are the same as in Table 3.1. R2, R4, R6 and R8 were first sampled on 12/04/2005. R1 and R2 have different y-axis scales.

During floods, the densities of 0+ fishes in backwaters (B1–B6; mean = 30 ± 43 fish m⁻²) were significantly higher than found in main river sites (R1–R8) during normal flows (Mann Whitney *U*-test: $Z = -3.751$, $n = 179$, $P < 0.000$). At the site level, the

maximum density of 0+ fishes in backwaters was 147 fish m⁻² at B5, followed by 104 fish m⁻² at B4 and 38 fish m⁻² at B2.

Substantial temporal variations in fish densities on the floodplains were observed. During the August 2004 flood, mean densities of 8 fish m⁻² and 11 fish m⁻² were recorded at F1 and F2 respectively. Extrapolating the densities found during sampling to the total area of the water in the floodplains at sampling (F1 = 2.0 hectares and F2 = 0.4 hectares), equates to approximately 16,000 and 4400 stranded fish respectively. Although there were floods of higher magnitude during winter months (October 2004, January 2005 and December 2006; Figure 3.2), the densities of fishes recorded on floodplains at these times were significantly lower than the densities found during the August 2004 flood (Mann Whitney *U*-test: F1 (1 fish m⁻²): $Z = -2.518$, $n = 12$, $P = 0.012$; F2 (<1 fish m⁻²): $Z = -2.236$, $n = 8$, $P = 0.025$).

3.3.3 Fish size

The bleak, roach and chub in backwaters (Table 3.3) and stranded on floodplains (Table 3.4) were generally larger than those captured during main river sampling prior to a particular flood event. Except during the January 2007 flood, when the first two species were larger in the river (Table 3.3). Significantly larger gudgeon (October 2005; independent samples *t*-test, $t = -8.877$, $P < 0.001$) and dace (December 2006; independent samples *t*-test, $t = -2.253$, $P = 0.025$) were found in backwaters than in the main river prior to each particular flood.

These differences were the result of an increase in the relative abundance of larger 0+ fish in backwaters and on the floodplains compared with in the river, rather than by an absence of smaller fish in the backwaters/floodplains (Figure 3.5). For example, bleak as small as 15mm SL and bream, chub and roach under 20mm SL were caught in backwaters during the January 2007 flood. In main river samples, the mean lengths of bleak and roach at some sites were significantly larger after floods than before (Table 3.5), suggesting that smaller fish had been displaced or were less likely to survive.

3.4 Discussion

Floods and high flow events in the Yorkshire Ouse had various effects on the habitat use and mortality of 0+ fishes, based on the timing and magnitude of the flood. Backwaters and areas of slack water provided refuge for high densities of 0+ fishes, irrespective of flood timing. A flood in late spring during the larval period (roach, dace, chub, perch and minnow) had negligible effects on relative abundance or community composition by the end of summer.

Artificial levees initially prevented the occupation of floodplains during flood events, but over-topping resulted in substantial numbers of 0+ fishes being stranded during summer floods. Backwaters and floodplains often supported larger fish than the main river, and fewer small fishes were caught after winter floods. The results are discussed below in relation to the resistance of 0+ fishes to flooding, based on the distribution of refuges, flood timing and, ultimately, the importance of lowland river rehabilitation.

Table 3.3 Comparison of bleak, chub and roach lengths (mean \pm CI, mm) between main river sites pre-flood and backwater sites during particular flood events

Flood timing	Bleak		Chub		Roach	
	River	Backwater	River	Backwater	River	Backwater
Aug-04	-	-	20.5 \pm 0.5	23.0 \pm 0.9 *** †††	23.5 \pm 0.7	22.3 \pm 0.5 ** ††
Oct-04	-	-	27.4 \pm 0.9	29.2 \pm 1.0 **	29.5 \pm 0.6	29.1 \pm 0.6
Oct-05	25.6 \pm 1.0	27.8 \pm 0.8 ** ††	27.5 \pm 1.3	27.5 \pm 0.7	29.9 \pm 0.8	29.6 \pm 1.0
	25.0 \pm 0.9	26.3 \pm 0.8 * †	22.2 \pm 1.1	26.9 \pm 2.1 ** ††	30.4 \pm 2.0	30.4 \pm 1.0
			25.7 \pm 1.0	29.3 \pm 1.0 *** †††	-	-
Dec-06	27.4 \pm 1.0	33.7 \pm 2.1 *** †††	26.2 \pm 1.2	29.7 \pm 1.1 *** †††	34.5 \pm 0.9	40.5 \pm 1.1 *** †††
	27.4 \pm 1.0	29.6 \pm 0.8 *** †††	-	-	34.5 \pm 0.9	35.3 \pm 2.3
	27.2 \pm 0.9	29.2 \pm 1.4 * †	-	-	31.9 \pm 1.1	30.9 \pm 0.7
	-	-	-	-	29.4 \pm 0.9	32.3 \pm 1.6 ** †
Jan-07	27.4 \pm 1.0	25.8 \pm 0.9 * ††	26.2 \pm 1.2	28.1 \pm 1.5	31.9 \pm 1.1	30.1 \pm 0.7 * ††
	27.2 \pm 0.9	26.1 \pm 0.5	-	-	-	-

Notes: * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$; t -tests and Mann-Whitney U -test if backwater mean/median fish length significantly different to river. † = $P < 0.05$, †† = $P < 0.01$, ††† = $P < 0.001$; two-sample Kolmogorov-Smirnov test if backwater length frequency distribution significantly different to river.

Table 3.4 Comparison of bleak, chub and roach lengths (mean \pm CI, mm) between main river sites pre-flood and floodplain sites during the August 2004 flood event

Site	Bleak		Chub		Roach	
	River	Floodplain	River	Floodplain	River	Floodplain
F1	-	-	20.5 \pm 0.5	23.7 \pm 0.5 *** †††	23.5 \pm 0.7	23.9 \pm 0.4
F2	20.8 \pm 0.7	23.0 \pm 0.4 *** †††	22.8 \pm 0.5	22.2 \pm 0.4 †	22.7 \pm 0.6	22.5 \pm 0.3 †
F3	18.8 \pm 0.5	20.2 \pm 0.9 ** †††	19.9 \pm 0.7	23.0 \pm 0.3 *** †††	20.9 \pm 0.4	21.5 \pm 0.4

Notes: * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$; t -tests and Mann-Whitney U -test if floodplain mean/median fish length significantly different to river. † = $P < 0.05$, †† = $P < 0.01$, ††† = $P < 0.001$; two-sample Kolmogorov-Smirnov test if floodplain length frequency distribution significantly different to river.

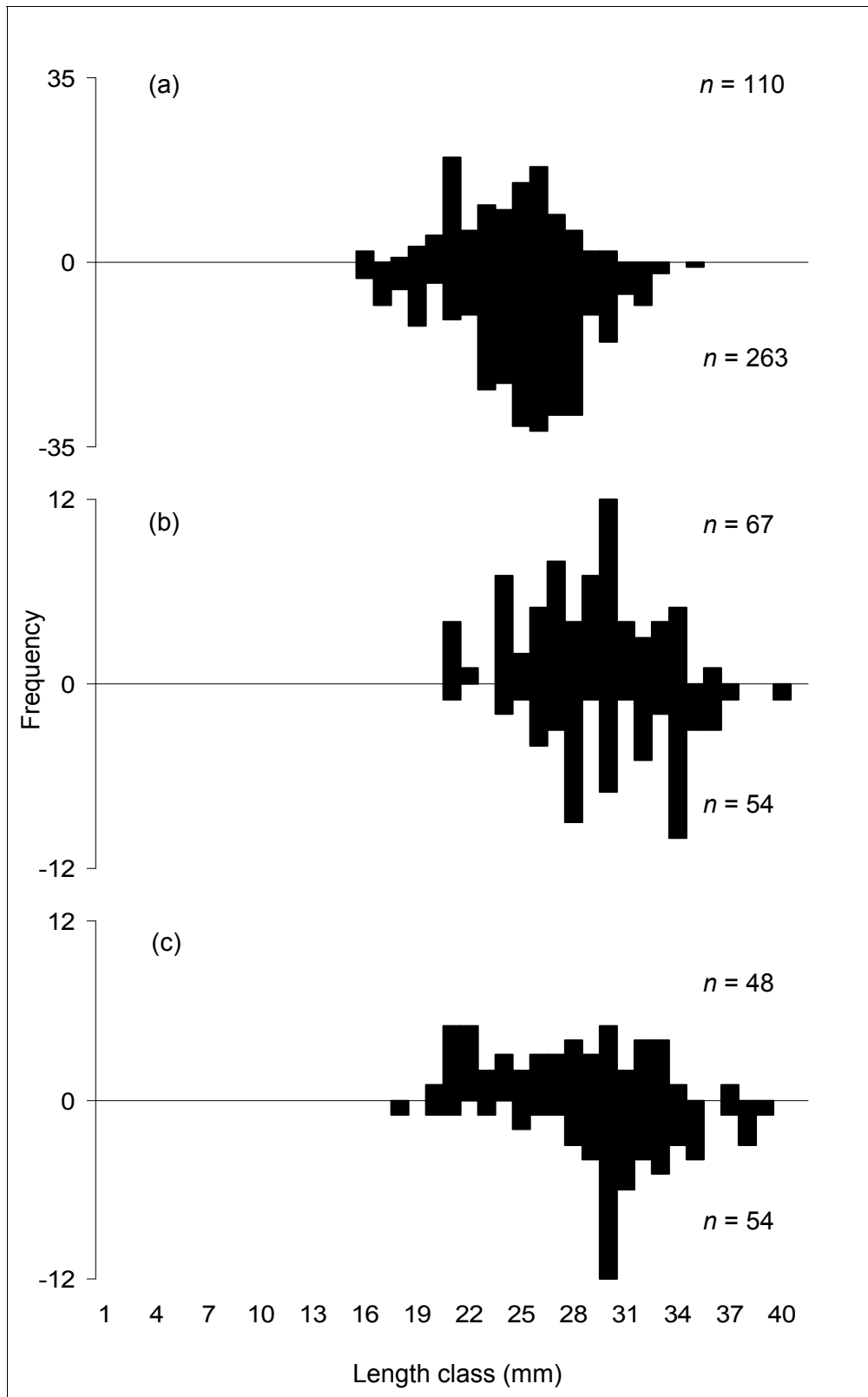


Figure 3.5 Comparative length-frequency distributions of chub catches from the river (top) and backwater/floodplain (bottom) when (a) similar median fish length but significantly different distribution (Aug 2004), (b) significantly different mean fish length but similar distribution (Oct 2004) and (c) significantly different mean fish length and distribution (Dec 2006)

Table 3.5 Comparison of fish lengths (mean \pm CI, mm) before and after particular winter flood events (growth assumed to be zero)

Flood date	Species	Sample site	Fish length (mean \pm CI, mm)	
			Before	After
October 2004	Dace	R1	38.1 \pm 0.9	39.0 \pm 0.9
January 2005	Roach	R5	28.7 \pm 0.4	29.6 \pm 1.2
October 2005	Bleak	R1	25.7 \pm 1.0	30.7 \pm 0.9 ***
	Chub	R1	27.4 \pm 1.3	28.9 \pm 0.8
	Gudgeon	R1	33.7 \pm 1.3	33.9 \pm 1.1
	Minnow	R1	26.1 \pm 0.8	25.6 \pm 0.9
	Roach	R1	29.9 \pm 0.8	32.7 \pm 1.2 ***
	Roach	R5	26.8 \pm 0.8	28.2 \pm 1.1
Winter 2006	Bleak	R7	26.0 \pm 0.7	29.8 \pm 1.1 ***
	Chub	R7	28.2 \pm 2.0	28.2 \pm 0.8
	Dace	R6	46.3 \pm 1.1	45.5 \pm 1.9
	Gudgeon	R6	46.2 \pm 1.1	44.3 \pm 2.0
	Roach	R7	30.6 \pm 1.0	31.3 \pm 1.2

Note: *** = $P < 0.001$; Mann-Whitney U -test if median fish length significantly different.

Pearsons *et al.* (1992) reported that fish populations were more stable in physically complex habitats because of the increased availability of flow refugia. Such areas are believed to enhance organism survival and recolonisation potential (Townsend 1989). During all the floods surveyed, high densities of 0+ fishes, including those that are strictly rheophilic, were found sheltering in backwaters and amongst riparian vegetation, thus avoiding displacement, physical damage and/or death. Numerous studies document the importance of riparian shelters for juvenile fishes, including rheophilic species (Baras *et al.* 1995; Grift *et al.* 2003; Schiemer *et al.* 2004; Humphries *et al.* 2006). Also, the importance of marginal slack waters for benthic-dwelling fishes increases when floods mobilise bed sediments (Lojkásek *et al.* 2005).

Fish species have evolved life-history strategies to survive floods based upon seasonal timing and predictability (synchronising a life-history stage to long-term flow regime dynamics; Poff and Allan 1995). For example, spawning can be timed so that hatching coincides with low flood probability (Seegrist and Gard 1972; Erman *et al.* 1988), because of the poor swimming capabilities of 0+ fish (Harvey 1987). Floods in the UK have generally been associated with heavy winter precipitation; summer floods are considered 'atypical' and a disturbance (Sparks *et al.* 1990). Climate change is likely to form a pattern of long-duration winter floods, with an increased incidence of short-term summer floods associated with storm events (Hulme *et al.* 2002).

During May 2006, elevated flows coincided with the larval period of roach, dace, chub, perch and minnow, but by the end of summer any impacts on diversity and species-specific relative abundance appeared to be minimal. Nevertheless, the long-term effects of such floods may be realised subsequently in the reduced abundance of adult fishes (Nunn *et al.* 2007b). This lack of a major impact may be because fish that survived the flood or hatched after the flood experienced reduced intra- and interspecific competition (Elwood and Waters 1969; Roghair *et al.* 2002), and also enjoyed a long period of hot and settled weather in midsummer.

Although not significant, the relative abundance of roach fell by the largest amount, perhaps due to the small size of the fish during the flood. Mann and Bass (1997) stated that the ability of 0+ roach and dace to hold station was positively related to fish length and water temperature, and negatively related to water velocity. Other studies have emphasised the importance of flood timing in relation to fish size and susceptibility to displacement and mortality (Harvey 1987; Mion *et al.* 1998; Jensen and Johnsen 1999; Nunn *et al.* 2007b).

Fish caught in backwaters and on floodplains during each of the floods were larger than those caught in the river. However, this may reflect ontogenetic shifts in habitat use (Copp 1992, 1997a; Garner 1996), especially if larger fish did not occupy marginal habitat at low flows and were thus under-represented in catches from the main river. Additionally, as fish increase in size through the summer they develop an escape response, meaning that the differences may be a result of investigator bias. Despite this, after the winter 2006 floods significantly larger roach and bleak were caught in the main river, again suggesting small fish were displaced or less likely to survive.

During the flood in August 2004, large numbers of fish were stranded on three different 'over-topped' floodplains, although fewer fish were found stranded after winter floods of greater magnitude. King *et al.* (2003) similarly documented stranding of larval and juvenile cyprinids after a summer flood. Habitat use of fish prior to the flood event was probably of fundamental importance, influencing lateral displacement and stranding. Juvenile cyprinid fish are known to select marginal habitats during summer months because they provide optimal temperature, feeding and predator avoidance (Garner 1997a, b; Baras and Nindaba 1999a, b), and are consequently more susceptible to lateral displacement. This is further supported by the lack of stranded gudgeon, which mainly occupy main channel benthic locations.

Fish were also found in managed floodplains – 'over-topped' levees that drain through flap gates, and sluice-filled and -drained water storage areas that are pumped dry after the floods recede. Although some fish were stranded in these areas, the majority of fish probably successfully returned to the main river through the flap gates and sluices. Sommer *et al.* (2005) suggested that mortality of young chinook salmon in isolated ponds of engineered water-control structures were relatively small in relation to the overall area of the floodplain. However, future floodplain rehabilitation or floodwater management structures should be designed so that all the water is allowed to drain back into the river, thus removing the risk of fish becoming stranded.

Furthermore, water should be able to return to the river quickly, to reduce potential mortality from piscivorous birds, low dissolved oxygen and high levels of tannins (Lusk *et al.* 1998; Fontenot *et al.* 2001; Henning *et al.* 2007). As the flood waters receded, large numbers of black-headed gull (*Larus ridibundus* L.; flocks up to 200) and carrion crow (*Corvus corone* L.; flocks up to 50) were observed on floodplains with isolated water, although it is believed they were feeding largely on slugs and worms that drowned during the floods rather than on stranded fish.

Cowx and Gerdeaux (2004) emphasised the need to recreate functional habitats for spawning, feeding, nursery (growth) and resting (self-protection), as well as the connectivity between these habitats, in order to improve the ecological functioning of the river system (Schiemer *et al.* 1999). This study provides empirical evidence for reinstating lowland river lateral connectivity and recreating habitat diversity and channel morphology (Cowx and Welcomme 1998), thus improving the ecological status of rivers under the WFD. Importantly, these restoration strategies do not focus on a single taxonomic group or species (Sparks 1995; Tockner *et al.* 2000). It is also important to recognise that floodplain rehabilitation increases system biodiversity, provides flood refuge and nursery areas for juvenile fish, and benefits society through the natural functional attributes of river landscapes for flood protection (Poff 2002; Tockner and Stanford 2002; Brenner *et al.* 2003).

4 Rehabilitation of lowland river-floodplain ecosystems: the importance of variable connectivity between man-made floodplain waterbodies and the River Trent

4.1 Introduction

Unmodified alluvial floodplain rivers have a high spatio-temporal heterogeneity of habitats along a gradient of lateral connectivity (flow of energy, matter and organisms; Ward *et al.* 2002c) with the main channel (Amoros *et al.* 1982). Consequently, there is a lotic-to-lentic succession of habitat moving from the main river channel into the floodplain, corresponding to a sequence of rheophilic-to-eurytopic-to-limnophilic fish species (Copp *et al.* 1991; Schiemer and Waidbacher 1992; Welcomme *et al.* 2006). The mosaic of different waterbodies, which vary in connectivity across the floodplain, are potentially characterised by distinctive fish assemblages that contribute to the overall high level of species diversity of riverine ecosystems (Copp 1989).

Flow regulation, channelisation and artificial levee construction (Ward 1998a; Amoros and Bornette 2002) invariably reduce rivers to single-thread channels and impede connectivity with their floodplains and lentic waters (Ward and Stanford 1995a; Cowx and Welcomme 1998). Such activities incur enormous losses in terms of fish spawning, production and nursery areas, potentially resulting in increasing numbers of endangered fish taxa (Schiemer and Waidbacher 1992; Jungwirth *et al.* 2002; Aarts and Nienhuis 2003).

The historic reductions in landscape connectivity, ecological functioning and ecosystem biodiversity detailed above have driven initiatives to improve the ecological status of rivers, such as the WFD. Achieving Good Ecological Status for degraded rivers involves activities such as rehabilitating the functional integrity (hydrological connectivity and habitat heterogeneity) and ecological processes of the river-floodplain complex, which are linked to high levels of biodiversity (Ward 1998a; Schiemer *et al.* 1999; Ward *et al.* 1999).

However, rehabilitation schemes rarely recognise the importance of variable floodplain connectivity, instead focusing efforts on improving high levels of connectivity in an attempt to maintain riverine fish community structure. For example, most studies have documented the importance of permanently-connected, man-made floodplain waterbodies as spawning, feeding, nursery (growth) and refuge areas for rheophilic species (Sabo and Kelso 1991; Neumann *et al.* 1994; Staas and Neumann 1996; Pinder 1997; Simons *et al.* 2001; Grift *et al.* 2003; Jurajda *et al.* 2004). In these studies, isolated floodplain waterbodies were often reconnected to the main river channel, invariably at the expense of distinct communities that were dependent on the lotic environment within floodplain waterbodies. Consequently, riverine ecosystem rehabilitation needs to account for variable levels of floodplain waterbody connectivity.

Moreover, many non-fish taxa attain different peak species richness along the lateral connectivity gradient (Tockner *et al.* 1998).

The aim of this study was to evaluate the importance of variable connectivity between man-made floodplain waterbodies and the River Trent for rehabilitating the riverine-floodplain ecosystem. Specifically, the study compared age 0+ fish species richness, diversity and composition across a gradient of floodplain connectivity and investigated the impact of man-made floodplain waterbodies on the overall community structure. The results are discussed in terms of the ecological requirements of lowland river fishes and the overriding processes influencing fish presence and distribution, including floods and human activity.

4.2 Materials and methods

4.2.1 Study site

The study was carried out on the lower River Trent in England (Figure 4.1). The River Trent is the third longest river in the UK (274km); it has a catchment area of 10,500km² and a long-term mean discharge of 84m³ s⁻¹. However, annual and seasonal variations do occur, such as the flood at the end of May 2006 (Figure 4.2). Historically, the River Trent was geomorphically active and prone to meander, but its channel has remained relatively stable in recent times, particularly since regulation of the river began approximately 300 years ago (Large and Petts 1996; Large and Prach 1998).

Currently, the lower Trent is channelised in many areas, and impounded by a number of large weirs and sluices. Overbank flooding occurs relatively infrequently because of the regulated nature of the river. In some areas, water depths are artificially maintained by periodic dredging to allow the transport of freight and the passage of pleasure craft, and much of the floodplain has been claimed for urban development or agriculture.

During the past decade, attempts have been made to re-establish the link between the lower reaches of the river and its floodplain by connecting a number of man-made waterbodies (such as flooded gravel quarries). These man-made floodplain waterbodies vary in their connection to the main river and can be grouped into three categories: (1) permanently connected (parapotamon); (2) connected during annual periods of elevated flow (plesipotamon); and (3) rarely connected by flood waters (paleopotamon).

The main aim of the restoration project was to increase the availability and diversity of habitat for fishes (including spawning and nursery habitat, and refuge from floods), particularly the early developmental stages. This was done with a view to enhancing fish recruitment success within the lower reaches of the river. To date, approximately 12 waterbodies have been connected to the lower reaches of the river, with more planned for the future.

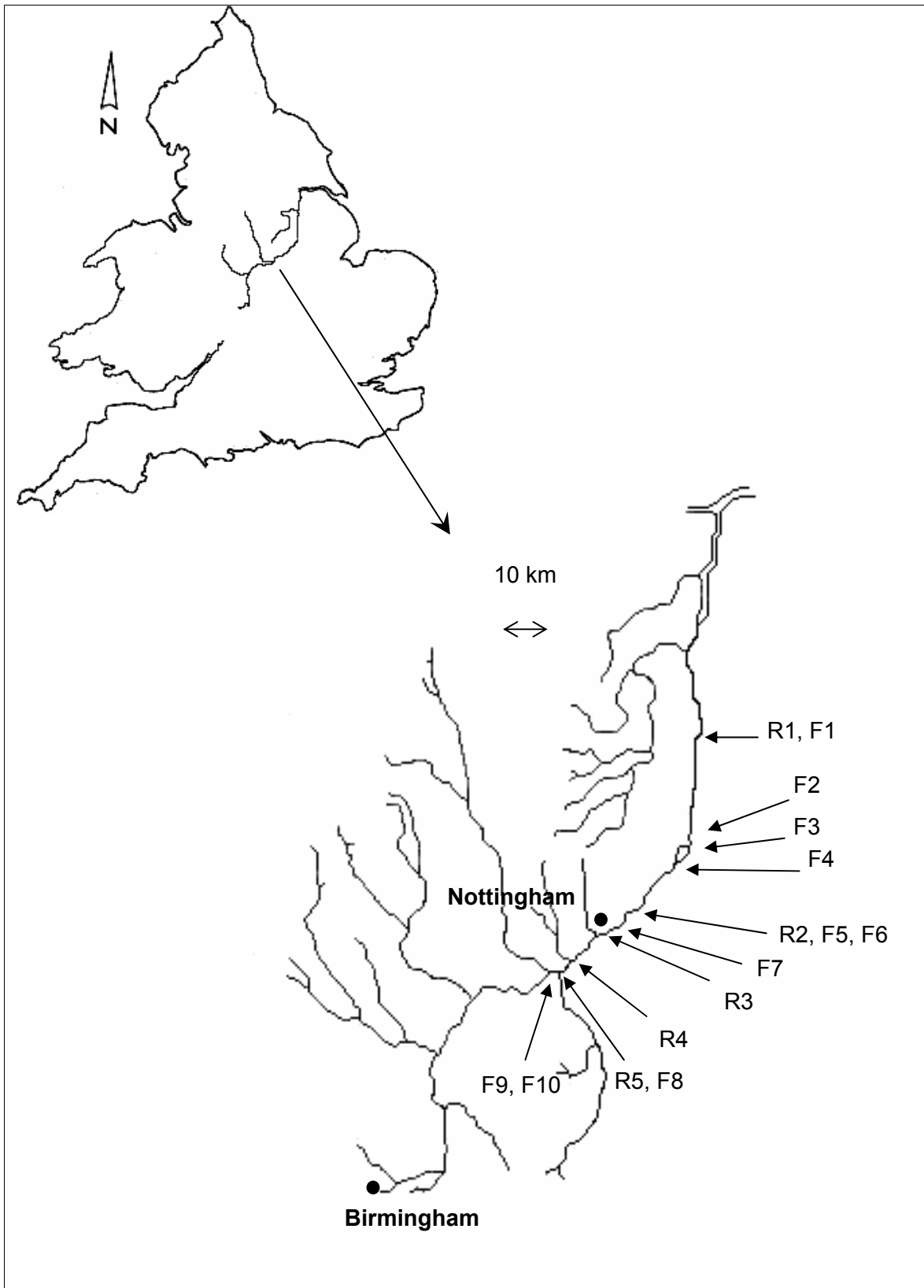


Figure 4.1 A map of England showing the location of the River Trent catchment, and a more detailed catchment map showing sampling sites (site codes are the same as in Table 4.1)

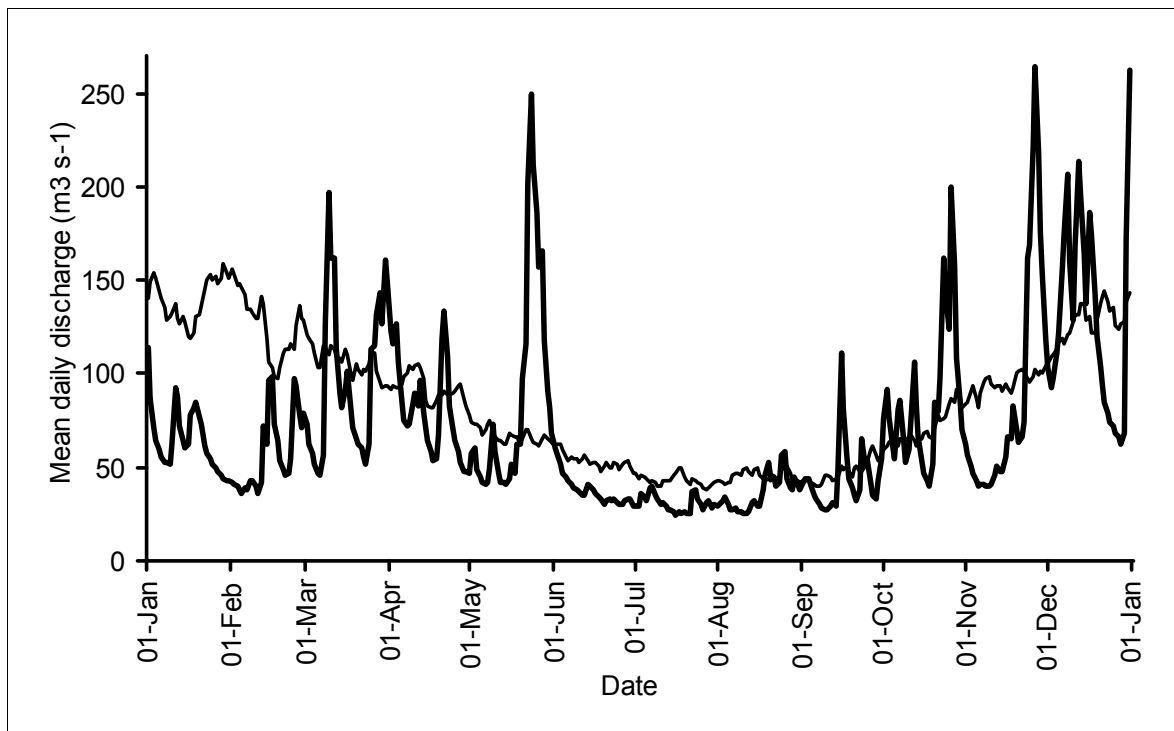


Figure 4.2 Mean daily discharge ($\text{m}^3 \text{s}^{-1}$) in the River Trent at Holme Pierrepont in 2006, compared with the long-term daily mean (thin line)

4.2.2 Surveys of 0+ fish

Populations of 0+ fish were surveyed in daylight hours at five river and 10 floodplain waterbody sites approximately fortnightly from May to July 2006 and monthly from August to November 2006 (Table 4.1). The connectivity varied between floodplain waterbodies (F), ranging from those permanently connected to the river (R) by deep, open channels to those connected only during 1.5m rises in river level. Connectivity was ranked based on the width (m), depth (m) and length (l) of the permanent connection or the river level required for temporary connection. Floodplain sites with the widest, deepest and shortest connecting channels were ranked higher than those with shallower, narrower and longer (or temporary) connecting channels (Table 4.1).

Connectivity rankings for F7 and F10 were adjusted to account for the distance of the sampling locations from the river and because fish access to the pond was impeded by dense vegetation. In all cases, sampling was restricted to areas devoid of large woody debris, in water $\leq 1.5\text{m}$ deep where the water velocity was slow and 0+ fishes tended to aggregate. All samples were collected using a micromesh seine net (25m long by 3m deep with a 3mm hexagonal mesh) that was set in a rectangle parallel to the bank by wading. The seine net captured larvae as small as 5mm, although its efficiency was reduced for fish smaller than around 15 mm (Cowx *et al.* 2001). Captured fish were identified to species (Pinder 2001), separated into six larval (L1–L6) and one 0+ juvenile (J) developmental steps (Copp 1990; Peñáz 2001), and measured for SL (nearest mm).

Table 4.1 Details of sites surveyed for 0+ fishes in the River Trent (R) and floodplain waterbodies (F), including river width (W, m), floodplain waterbody area (A, ha), maximum depth (Max. D, m), dimensions of connectivity channel (W = width, D = depth and L = length, m) or river level rise required for connection (m), connectivity rank (see text for details), substratum and key aquatic macrophytes

Site name	Habitat	Code	Dimensions		Connection channel		Substratum	Key aquatic macrophytes
			W (m) / A (ha)	Max. D (m)	L x W x D / river level rise (m)	Rank		
Dunham	Main river	R1	100	3–4	-	-	Gravel, mud	<i>Phalaris arundinacea</i> L.
Holme Pierrepont	Main river	R2	75	3–4	-	-	Sand, gravel	<i>Schoenoplectus lacustris</i> (L.), <i>Glyceria maxima</i> (Hartm.)
Trent Bridge	Main river	R3	75	3–4	-	-	Mud, silt	-
Attenborough	Main river	R4	100	3–4	-	-	Sand, gravel	<i>Acorus calamus</i> L., <i>G. maxima</i> , <i>Sparganium erectum</i> L.
Thrumpton	Main river	R5	75	3–4	-	-	Sand, gravel	<i>G. maxima</i> , <i>S. erectum</i>
Dunham Lake	Floodplain	F1	2	3	1.5	10	Mud, silt	<i>P. arundinacea</i>
Winthorpe Lake	Floodplain	F2	6	4	50 x 2 x 1	3	Sand, silt	<i>A. calamus</i> , <i>Butomus umbellatus</i> L., <i>G. maxima</i> , <i>S. erectum</i>
Binghams Pond	Floodplain	F3	2.5	3	40 x 2 x 1	2	Gravel, silt	<i>G. maxima</i>
Farndon Pond	Floodplain	F4	0.5	2	30 x 2 x 0.4	4	Sand, silt	<i>G. maxima</i> , <i>Phragmites australis</i> Trin.
Marina Pond	Floodplain	F5	3	3	0.1	7	Gravel, silt	<i>Potamogeton pectinatus</i> L.
Marina Pond	Floodplain	F6	3	3	0.1	6	Gravel, silt	<i>P. pectinatus</i>
Cowlick Marina	Floodplain	F7	1	3	30 x 20 x 3	5	Silt, concrete	<i>A. calamus</i> , <i>G. maxima</i> , <i>Lemna minor</i> L., <i>S. erectum</i>
Thrumpton Pond	Floodplain	F8	0.5	1.5	0.5	8	Mud, silt	<i>Elodea canadensis</i> Michx.
Ully Gully	Floodplain	F9	1	1.5	0 x 7 x 0.7	1	Mud, silt	<i>G. maxima</i> , <i>P. arundinacea</i>
Glazebrook Pond	Floodplain	F10	0.8	4	50 x 1.5 x 0.2	9	Sand, silt	<i>G. maxima</i>

4.2.3 Data analysis

For each site (all samples combined), the number of species caught (alpha diversity), the turnover of species between each floodplain waterbody and the nearest river site (beta diversity, Whittaker's measure) and the overall number of species caught from all sites (gamma diversity) were calculated (Magurran 1988). Whittaker's measure of beta diversity (βW) was calculated as:

$$\beta W = (S/\alpha) - 1 \quad (4.1)$$

where S is the total number of species present along the gradient and α is the average number of species caught (Magurran 1988). The frequency of occurrence and relative abundance of each fish species (Hynes 1950), the Shannon-Wiener diversity index (H'), species richness and Pielou's measure of evenness (J) (Washington 1984) from all the surveys at each site, and the relative density (fish m^{-2}) of 0+ fishes (all species combined) were also calculated for each sampling occasion.

The frequency of occurrence of a given species was defined as the number of surveys in which the species occurred, expressed as a frequency of the total number of surveys in which fish were captured. Relative abundance of a species was defined as the percentage of total catches (numbers) in all surveys accounted for by the given species. Species-specific abundance was defined as the percentage of all fish accounted for by the given species in those surveys where the species occurred.

Species composition of 0+ fish catches was analysed for all sites using the graphical method of Costello (1990), as modified by Amundsen *et al.* (1996). This involved plotting species-specific abundance against the frequency of occurrence at each site. The relative density of 0+ fishes was calculated by dividing the total numbers of 0+ fishes captured by the known area sampled by the net on each sampling occasion at each site (the area was calculated from direct *in situ* measurements of the study sites).

To investigate the similarity in 0+ fish species composition between sites, a Bray-Curtis similarity matrix of mean percentages for each 0+ fish species was calculated and presented as a dendrogram using hierarchical agglomerative clustering (group average linkage; PRIMER, version 6). The index ranges from 0 (no species in common) to 1 (identical samples), with a value of 0.6 (60% similarity) taken as an indication of significant species overlap between samples (Zaret and Rand 1971; Garner 1996).

Mann-Whitney U -tests were used to test the null hypotheses that median H' , richness, J and density of 0+ fishes for all surveys at each site did not differ significantly between the river and floodplain sampling units. Spearman rank correlation tests were used to test the null hypotheses that floodplain waterbody connectivity was not significantly correlated with alpha diversity, beta diversity, H' , richness and J . Statistical analyses were carried out using SPSS (version 15.0) with a significance level $\alpha = 0.05$.

4.3 Results

4.3.1 Species composition

More than 555,700 specimens of 25 fish species (gamma diversity) were captured during the study period (Table 4.2). Of these, 22 species (almost 220,000 individuals) were caught from the main river and 22 species (over 336,000 individuals) were caught from floodplain waterbodies. Brown trout (*Salmo trutta* (L.)), flounder (*Platichthys flesus* (L.)) and common goby (*Pomatoschistus microps* (Krøyer)) were only captured from the main river, while three limnophilic species – ten-spined stickleback (*Pungitius pungitius* (L.)), rudd and tench (*Tinca tinca* (L.)) – occurred exclusively in floodplain waterbodies. Dace (38%), roach (18%) and chub (17%) were most abundant in main river catches, with dace (92%), roach (85%), gudgeon (65%), perch (65%) and chub (65%) occurring most frequently (Table 4.2). Roach (37%), perch (22%) and dace (9%) were the most abundant species in floodplain waterbodies and also occurred most frequently (roach = 72%, perch = 61% and dace = 58%; Table 4.2).

The number of species captured in individual floodplain waterbodies (alpha diversity) was positively correlated to connectivity (Spearman rank: $r = 0.829$, $n = 10$, $P = 0.003$), with reduced connectivity leading to a decline in the presence of rheophilic species (Table 4.2). Adult bream, perch, carp (*Cyprinus carpio* (L.)), roach and pike (*Esox lucius* (L.)) were captured in floodplain waterbodies in early summer (spawning period), and probably contributed to the dominance of 0+ eurytopic species in subsequent catches. Furthermore, >0+ rudd and tench were captured in floodplain waterbodies on numerous occasions, along with low numbers of 0+ limnophilic species (Figure 4.3). Beta diversity increased along the gradient of decreasing floodplain waterbody connectivity as the species composition became increasingly dissimilar to the nearest river site, although the trend was not significant (Spearman rank: $r = -0.497$, $n = 10$, $P = 0.144$).

The community structure of 0+ fish varied between sites, both in the river (Figure 4.4) and the floodplain waterbodies (Figure 4.5). For example, R1 was characterised by dace (species-specific abundance = 36%), roach (19%), chub (19%), bleak (15%) and gudgeon (7%), with perch captured in 78% of surveys but in smaller numbers. Whereas in R2 dace, perch and roach accounted for 73%, 17% and 4% of catches, respectively.

Using the Bray-Curtis similarity index based on the mean relative abundance (%) of each 0+ fish species at each site, eight main groups possessing 0+ fish communities that were at least 60% similar were identified (Figure 4.6a). One group contained R2, R3 and F7 (dominated by dace), one contained R1, R4 and F3 (roach, dace and chub), one contained F4, F5 and F10 (roach), and one contained F2 and F6 (perch). There were also four dissimilar sites: R5 (chub and roach), F9 (minnow), F8 (three-spined (*Gasterosteus aculeatus* (L.)) and ten-spined sticklebacks) and F1 (carp and bream).

These groups of sites correspond approximately to the degree of floodplain waterbody connectivity, with poorly connected waterbodies containing fish species compositions that are highly dissimilar to river sampling sites (Figure 4.6b). The exceptions to the trend were F7 and F3, which were both permanently connected to the main river but contained larger proportions of rheophilic fish than waterbodies with similar connectivity rankings.

Table 4.2 Relative abundance of 0+ fish captured from five main river sites (R1–R5) and ten floodplain waterbodies (F1–F10) on the River Trent

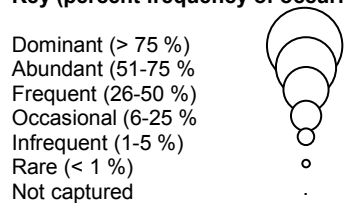
Family	Ab. ¹	Vernacular name	Flow	Site code															
				Flow pref. ¹	R1	R2	R3	R4	R5	F1	F2	F3	F4	F5	F6	F7	F8	F9	F10
Balitoridae																			
<i>Barbatula barbatula</i> (L.)	Bt	Stone loach	Rheo A	o	-	o	o	-	-	-	o	-	-	-	-	o	-	o	-
Cobitidae																			
<i>Cobitis taenia</i> L.	Ct	Spined loach	Rheo B	-	o	-	o	o	o	o	o	-	-	-	-	o	-	o	-
Cottidae																			
<i>Cottus gobio</i> L.	Cg	Bullhead	Rheo A	-	o	o	o	o	o	-	o	-	o	-	-	o	-	-	-
Cyprinidae																			
<i>Barbus barbus</i> (L.)	Bb	Barbel	Rheo A	o	-	-	o	o	o	-	o	o	-	-	-	-	-	-	-
<i>Rhodeus sericeus</i> (Pallas)	Rs	Bitterling	Limno	-	-	-	-	o	o	-	-	-	-	-	-	-	-	o	-
<i>Alburnus alburnus</i> (L.)	Aa	Bleak	Eury	o	o	o	o	o	o	-	o	o	o	o	o	o	o	o	o
<i>Abramis brama</i> (L.)	Ab	Bream	Eury	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o
<i>Cyprinus carpio</i> L.	Cc	Carp	Eury	-	-	-	o	-	-	o	o	-	o	-	-	-	-	-	o
<i>Leuciscus cephalus</i> (L.)	Lc	Chub	Rheo A	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o
<i>Leuciscus leuciscus</i> (L.)	Ll	Dace	Rheo A	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o
<i>Gobio gobio</i> (L.)	Gg	Gudgeon	Rheo B	o	o	o	o	o	o	-	o	o	o	o	o	o	o	o	o
<i>Phoxinus phoxinus</i> (L.)	Pp	Minnnow	Rheo A	o	o	o	o	o	o	-	o	o	o	o	o	o	o	o	o
<i>Rutilus rutilus</i> (L.)	Rr	Roach	Eury	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o
<i>Scardinius erythrophthalmus</i> (L.)	Se	Rudd	Limno	-	-	-	-	-	-	-	o	-	o	-	-	-	-	-	o
<i>Abramis bjoerkna</i> (L.)	Aj	Silver bream	Eury	o	-	-	-	-	-	-	-	-	-	-	o	-	-	-	-
<i>Tinca tinca</i> (L.)	Tt	Tench	Limno	-	-	-	-	-	-	-	-	-	-	-	-	-	-	o	-
Esocidae																			
<i>Esox lucius</i> L.	El	Pike	Eury	-	-	-	o	o	o	o	-	o	o	o	-	o	o	o	o

Table 4.2 (cont.)

Family <i>Species</i>	Ab. ¹	Vernacular name	Flow pref. ²	Site code															
				R1	R2	R3	R4	R5	F1	F2	F3	F4	F5	F6	F7	F8	F9	F10	
Gasterosteidae																			
<i>Gasterosteus aculeatus</i> L.	Ga	Three-spined stickleback	Eury	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o
<i>Pungitius pungitius</i> (L.)	Pp	Ten-spined stickleback	Limno	-	-	-	-	-	-	-	o	o	-	-	-	-	o	o	o
Gobiidae																			
<i>Pomatoschistus microps</i> (Krøyer)	Pm	Common goby		o	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Percidae																			
<i>Gymnocephalus cernuus</i> (L.)	Gc	Ruffe	Eury	-	-	o	o	-	-	-	o	o	o	o	o	-	-	o	-
<i>Perca fluviatilis</i> L.	Pf	Perch	Eury	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o
<i>Sander lucioperca</i> (L.)	Sl	Zander	Eury	-	o	o	o	-	-	-	o	-	o	o	o	o	-	-	-
Pleuronectidae																			
<i>Platichthys flesus</i> (L.)	Pf	Flounder	Rheo C	o	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Salmonidae																			
<i>Salmo trutta</i> L.	St	Brown/sea trout	Rheo A	-	-	o	-	-	-	-	-	-	-	-	-	-	-	-	-

Notes: 1. Ab. = species abbreviation. 2. Flow preference classification according to Schiemer and Waidbacher (1992) – Rheo A = rheophilic A, Rheo B = rheophilic B, Eury = eurytopic and Limno = limnophilic. Site codes are as in Table 4.1.

Key (percent frequency of occurrence and abundance)



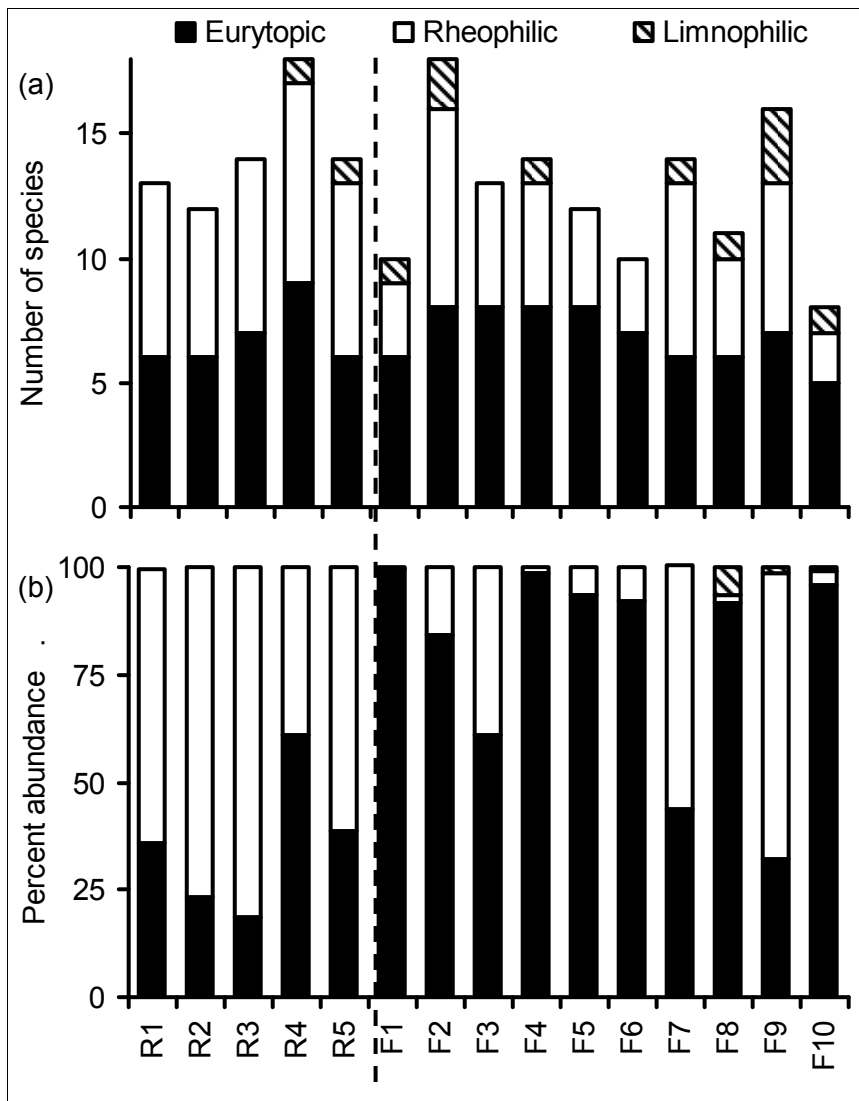


Figure 4.3 Number (a) and percent abundance (b) of rheophilic, eurytopic and limnophilic species captured from five main river sites (R1–R5) and ten floodplain waterbodies (F1–F10) on the River Trent

Notes: Flow preference classification according to Schiemer and Waidbacher (1992). Site codes are as in Table 4.1.

H' (2.05), richness (1.81) and J (0.64) from all surveys in the Trent catchment (main river and floodplain sites) were high, but between-site variations occurred (see Table 4.3). Median H' (Mann-Whitney U -test: $Z = -0.1225$, $n = 15$, $P = 0.254$), richness (Mann-Whitney U -test: $Z = -0.1592$, $n = 15$, $P = 0.129$) and J (Mann-Whitney U -test: $Z = -0.621$, $n = 15$, $P = 0.594$) were not significantly different between the main river and the floodplain sites. Connectivity had a strong correlation with species richness within the floodplain (Spearman rank: $r = 0.879$, $n = 10$, $P = 0.001$). H' decreased with decreasing hydrological connectivity, but the trend was not significant (Spearman rank: $r = 0.491$, $n = 10$, $P = 0.150$).

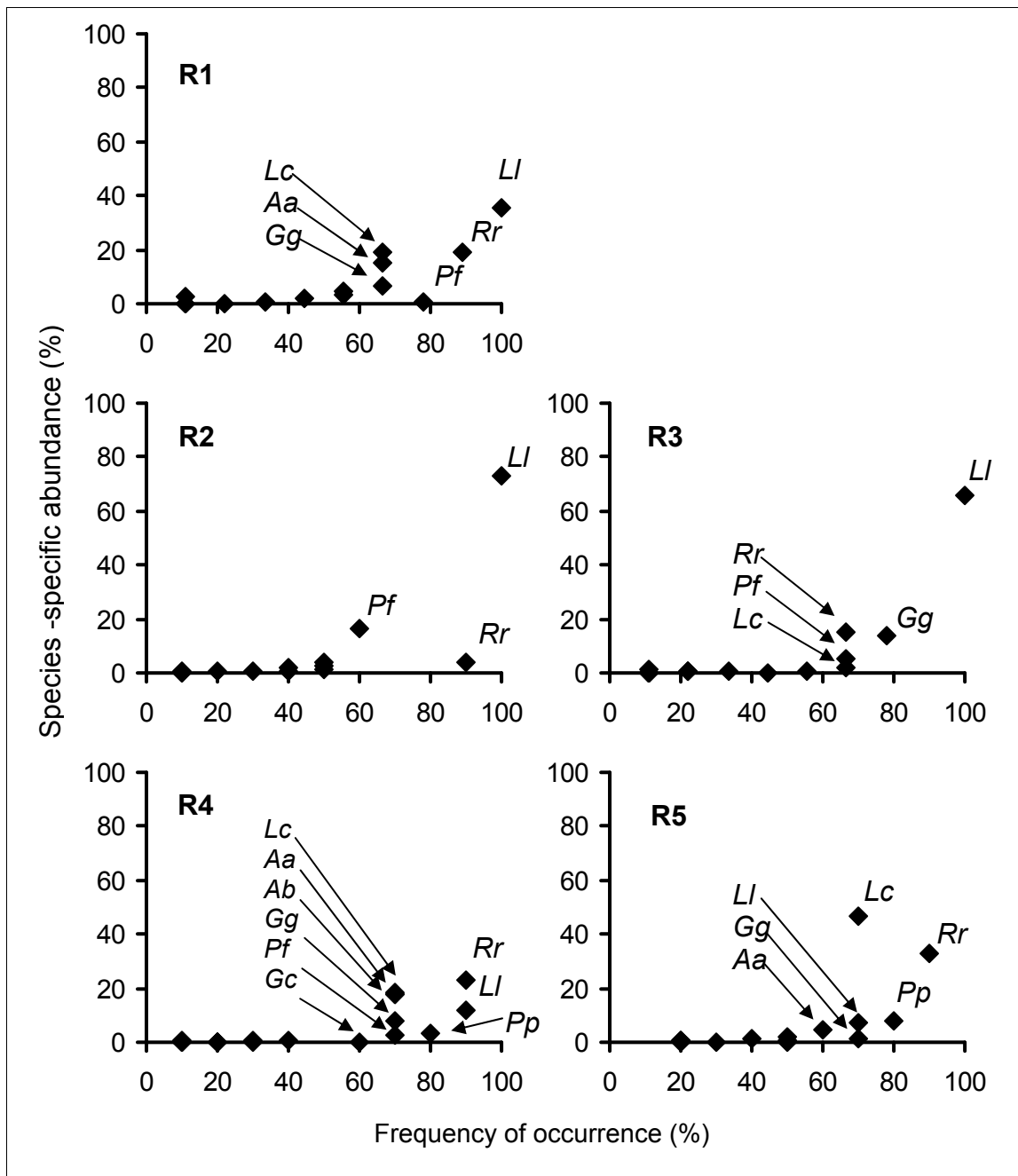


Figure 4.4 Costello plots demonstrating 0+ fish community structure at five main river sites on the River Trent

Note: Site name abbreviations are as in Table 1; species name abbreviations are as in Table 4.2.

4.3.2 Density

Overall, the mean (\pm SD) density of 0+ fishes (all river and floodplain sites combined) was 60 ± 143 fish m^{-2} . The highest mean (260 ± 258 fish m^{-2}) and maximum (921 fish m^{-2}) densities were found at R4 and F2, respectively, and the lowest mean density was found at F10 (3 ± 5 fish m^{-2}). The mean density of 0+ fishes in the main river (71 ± 155 fish m^{-2}) was not significantly different to the densities in permanently-connected (73 ± 166 fish m^{-2} ; Mann-Whitney *U*-test: $Z = -0.365$, $n = 11$, $P = 0.792$) and occasionally-connected (28 ± 63 fish m^{-2} ; Mann-Whitney *U*-test: $Z = -0.490$, $n = 9$, $P = 0.730$) floodplain waterbodies, but substantial spatial (between sites) and temporal (within a site) variations occurred (Figures 4.7 and 4.8).

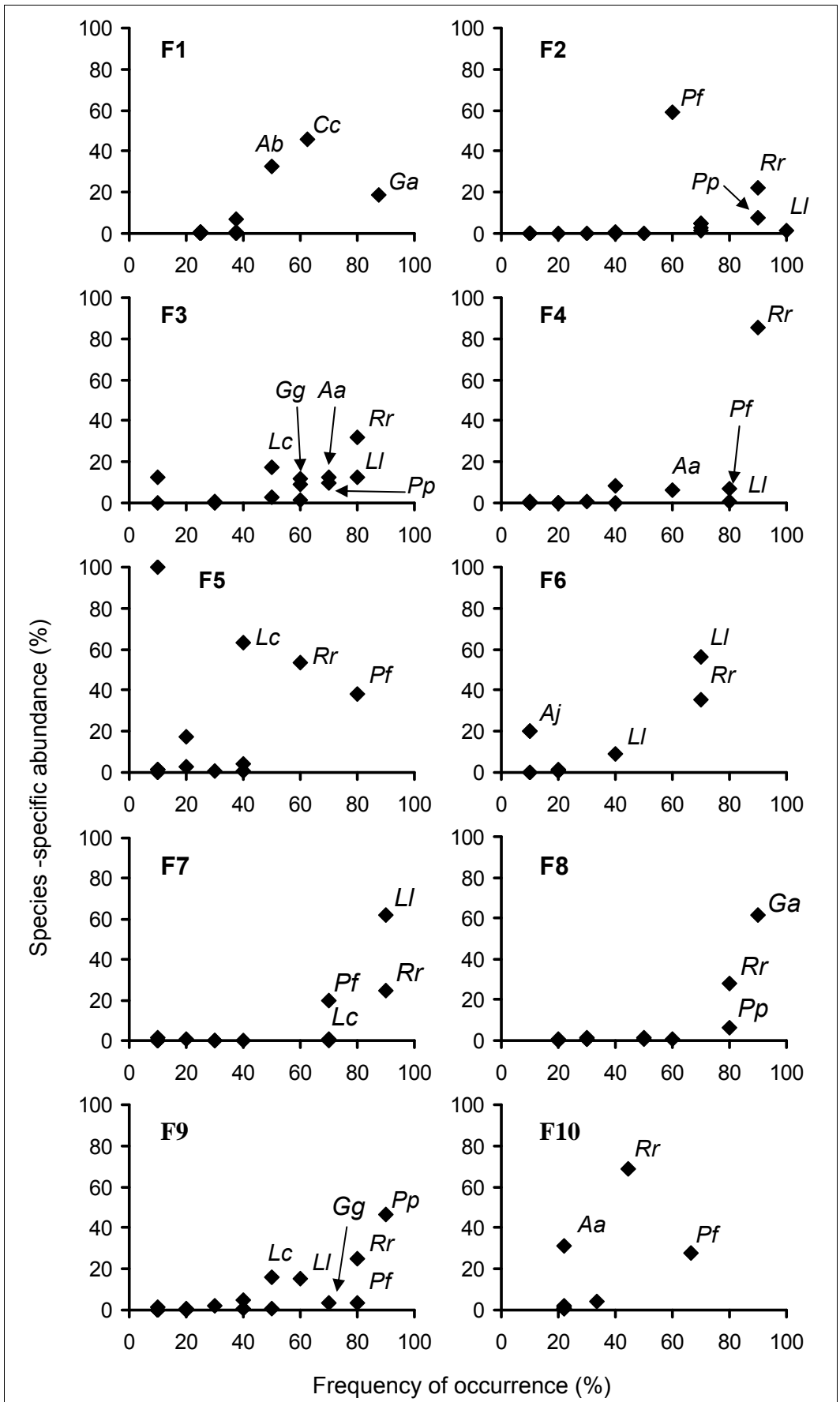


Figure 4.5 Costello plots demonstrating 0+ fish community structure at 10 floodplain waterbodies on the River Trent
 Note: Site name abbreviations are as in Table 4.1; species name abbreviations are as in Table 4.2.

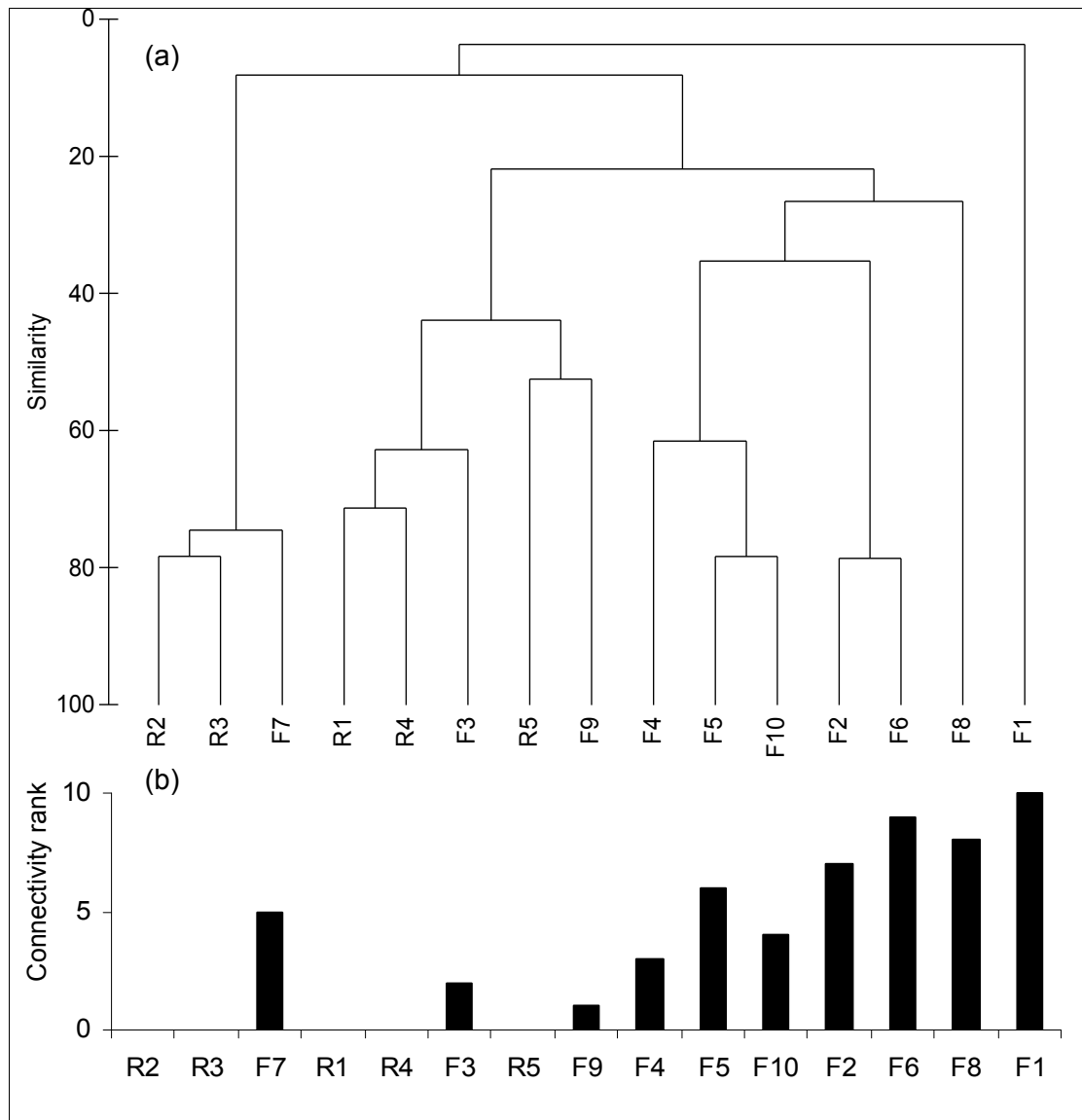


Figure 4.6 Similarity (a) of 0+ fish species composition between five main River Trent (R) and 10 floodplain waterbodies (F) of variable connectivity (b)

Notes: Site codes are as in Table I. Note low connectivity rank = highly connected.

Densities of 0+ fishes were low in May and early June (immediately after the flood; Figure 4.2), but increased and generally peaked in June and July, once the majority of species had hatched and grown to a size that could be efficiently captured by the seine net. Densities of 0+ fishes declined at most sites during August and September, as biotic (predation, disease, starvation) and abiotic (light, temperature, flow, nutrients) factors acted upon the populations, and 0+ fishes dispersed from the margins.

Table 4.3 Shannon-Wiener diversity index (H'), species richness and Pielou's measure of evenness (J) for all samples from five main river sites (R1–R5) and 10 floodplain waterbodies (F1–F10), and beta diversity (βW) between floodplain waterbodies and local river sampling sites on the River Trent

	Site code															
	R1	R2	R3	R4	R5	F1	F2	F3	F4	F5	F6	F7	F8	F9	F10	
H'	1.76	0.94	1.10	1.92	1.43	1.19	1.41	1.96	0.63	1.10	0.93	1.08	1.03	1.52	0.89	
Richness	1.52	1.14	1.35	1.41	1.45	1.00	1.48	1.34	1.20	1.25	1.03	1.14	0.93	1.52	0.92	
J	0.67	0.38	0.42	0.66	0.54	0.52	0.49	0.77	0.24	0.44	0.40	0.41	0.43	0.55	0.43	
βW	-	-	-	-	-	0.50	0.20	0.28	0.15	0.25	0.27	0.19	0.20	0.20	0.36	

Site codes are the same as in Table 4.1.

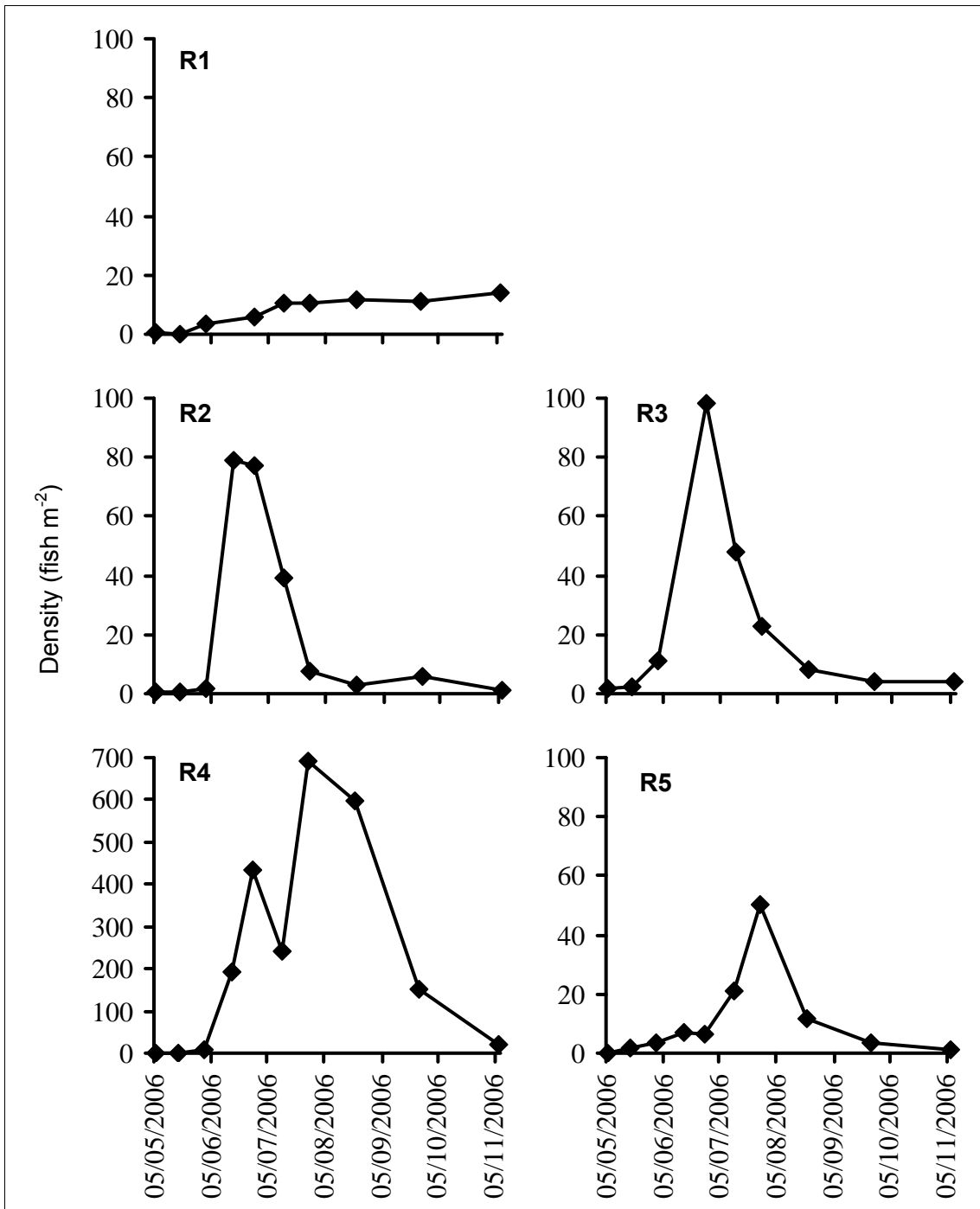


Figure 4.7 Temporal variations in the density (fish m⁻²) of 0+ fishes (all species combined) at five main river sites on the River Trent

Notes: Site codes are as in Table 4.1. R4 has a different y-axis scale.

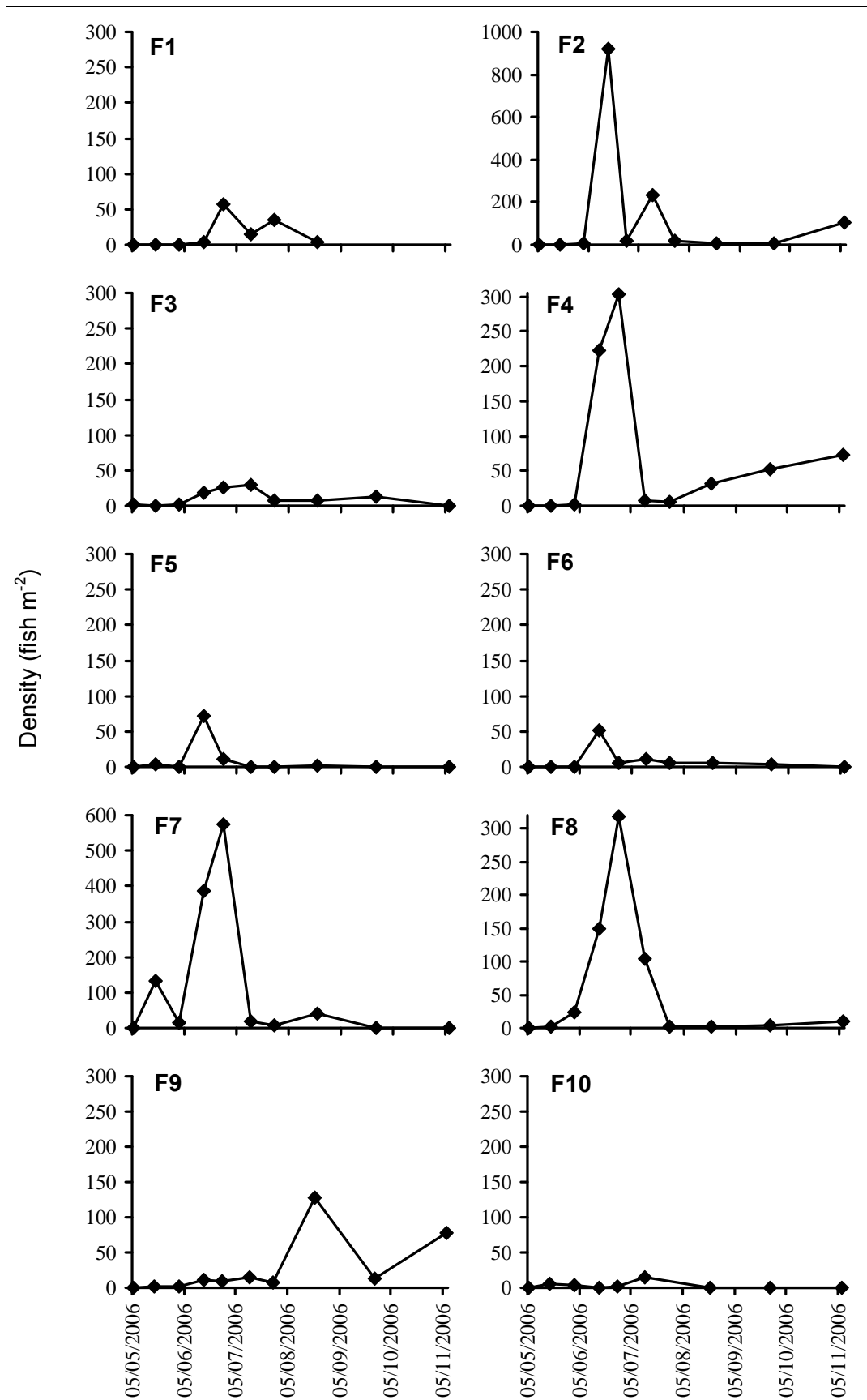


Figure 4.8 Temporal variations in the density (fish m⁻²) of 0+ fishes (all species combined) at 10 floodplain sites on the River Trent

Notes: Site codes are as in Table 4.1. F2 and F7 have different y-axis scales.

4.4 Discussion

The effective management and restoration of riverine floodplains requires understanding how species distributions are produced by considering how natural and man-made floodplain waterbodies function in other catchments. In the River Trent, local (alpha) and overall (gamma) species diversity, richness, turnover (beta diversity) and guild composition of fish communities in 10 man-made floodplain waterbodies are influenced by variable hydrological connectivity to the river.

Hydrological connectivity is the transfer of water between the river channel and the floodplain, and thus determines the ease with which organisms, matter or energy traverse the ecotones between the main river and the floodplain waterbody (Ward *et al.* 1999). During the study on the River Trent, man-made habitats ranged from waterbodies with a permanent connection to the river (parapotamon), those temporarily connected during elevated river levels (plesipotamon) and those with no connection (paleopotamon).

This broad spectrum of connectivity produced habitats similar to a natural riverscape. Consequently, species richness and diversity (alpha and beta) compared favourably with studies of unmodified river reaches. For example, Tockner *et al.* (1998) found that fish species richness in floodplain waterbodies declined with increasing distance from the main channel of the River Danube. Ward *et al.* (1999) reported that the alpha diversity of fish community composition decreased while the beta diversity increased with increasing isolation of Danubian floodplain waterbodies.

The species compositions of the waterbodies in this study were similar to natural riverscapes (Copp 1989), reflecting the ecological requirements and life-history strategies of lowland river fish species. In the River Trent, fish communities in highly-connected floodplain waterbodies were composed of a large proportion of eurytopic fishes and moderate numbers of rheophilic species (especially dace). In natural floodplains, eurytopic adults engage in spawning migrations from the main river into connected waterbodies, while 0+ fish spawned in the main river (eurytopic and rheophilic) disperse into connected floodplain waterbodies (Hohausova 2000; Borchering *et al.* 2002; Hohausova *et al.* 2003). Such movements allow young progeny to take advantage of abundant food resources and find a refuge from fast-flowing water (the Inshore Retention Concept; Schiemer *et al.* 2001).

The findings of this study support the conclusions of earlier investigations on the importance of permanently-connected man-made floodplain waterbodies in providing essential spawning, nursery and feeding habitat (for example, Sabo and Kelso 1991; Neumann *et al.* 1996; Staas and Neumann 1996; Copp 1997b; Pinder 1997; Pinder *et al.* 1997; Grift *et al.* 2003; Nunn *et al.* 2007a).

Along the gradient of reduced floodplain waterbody connectivity, the number of species declined in line with the inability of rheophilic species to disperse from their lotic spawning habitat in the main river (Schiemer and Waidbacher 1992). Large proportions of eurytopic species were present in the main river and at all levels of floodplain waterbody connectivity, reflecting their flexibility towards spawning and other habitat prerequisites.

The largest relative abundance of bream was found in Dunham Lake (F1), which remained permanently disconnected during the study period. Molls (1999) found that adult bream develop permanent stocks in oxbow lakes on the River Rhine because of the irregularity of connection. Thus, in low flow years, bream have a reproductive advantage over other fish species that require seasonal timing of connectivity, but they are unable to perform lateral spawning migrations. Limnophilic species were found in seven of the floodplain waterbodies, probably because the areas provided dense vegetation and the low-flow environment necessary for larvae and juveniles (Copp

1993; Copp and Mann 1993; Aarts *et al.* 2004). Bitterling (*Rhodeus sericeus* (Pallas)) was the only limnophilic species caught in the main river. However, the presence of unionid mussels for spawning has an overriding influence on its distribution (Smith *et al.* 2004), although the bitterling could have been washed-out or dispersed from local floodplain waterbodies.

The distribution of 0+ fish species may have been affected by the flood in May 2006 (Chapter 3). In the UK, summer floods are considered 'atypical' and a disturbance (Sparks *et al.* 1990) because of the poor swimming capabilities of 0+ fishes (Harvey 1987). Dace, roach and perch all hatched at least two weeks prior to the May flood and were among the most abundant species in 2006. This finding suggests that these species had reached a sufficient size to hold station (Harvey 1987; Mann and Bass 1997; Nunn *et al.* 2007b) or find suitable flow refuge during the flood (Chapter 3; Baras *et al.* 1995; Griff *et al.* 2003; Schiemer *et al.* 2004; Humphries *et al.* 2006).

The presence of 0+ rheophilic species in previously unconnected floodplain waterbodies during summer 2006 suggests that river fishes were displaced laterally and could take advantage of different floodplain habitats for refuge (Sedell *et al.* 1990; Molls and Neumann 1994; Copp 1997b; Pinder *et al.* 1997). Despite this, densities of fishes in all floodplain waterbodies immediately after the flood were low, suggesting that most fish had moved back into the river as the floodwaters receded or had been dispersed from the usual sampling locations by the flood.

Floodplain waterbody connectivity did appear to influence 0+ fish species composition, but numerous abiotic (pH, water temperature, nutrient content, suspended solids/turbidity, dissolved oxygen, lake morphology) and biotic (predation and competition) factors could also have had an effect on assemblage structure (Amoros and Bornette 2002). Furthermore, it needs to be recognised that man-made floodplain waterbodies undergo a process of succession, in which newly-created waterbodies will consist of opportunistic, highly-tolerant generalists (Lake *et al.* 2007). This means that the species compositions observed during the study may not persist. For example, the dominance of three-spined stickleback in the relatively recently created (2003) Thrumpton Pond (F8) may not persist.

Similarly, the emphasis of this study was on restoring habitat diversity based on the assumption that biotic composition and function will self-assemble: if you build it, they will come ('The Field of Dreams approach' *sensu* Hilderbrand *et al.* 2005). However, particular species may not have the ability to colonise poorly-connected habitats and/or the regional species pool may not be sufficient to return to an historical natural state (Lake *et al.* 2007). In the River Trent, however, relatively rare limnophilic fishes were present in numerous floodplain waterbodies of variable connectivity, thus alleviating the concerns proposed by Lake *et al.* (2007).

Guidelines for holistic riverine ecosystem management implicitly state the need for restoring the spatio-temporal diversity and functional integrity of the river-floodplain complex, as it is responsible for high levels of biodiversity (Ward 1998a; Schiemer *et al.* 1999; Ward *et al.* 1999). This study provides evidence of the importance of variable connectivity between the main river and man-made floodplain waterbodies in rehabilitating the lowland river fish community. Fish assemblages (ecological guilds, species and developmental stages) with different environmental requirements contributed to a high overall level of species diversity, resembling natural floodplain ecosystems.

This knowledge has crucial implications for improving the ecological status of rivers under the WFD. Furthermore, as overall biodiversity is highest at intermediate levels of floodplain connectivity (Tockner *et al.* 1998), the restoration of variable connectivity should not focus on a single species or taxonomic group (Sparks 1995; Tockner *et al.* 2000a). This study confirms the benefits of incorporating man-made floodplain

waterbodies of variable, not just high, levels of hydrological connectivity into holistic riverine ecosystem management plans.

5 Imaging fish activity at a lowland river-backwater connection during elevated flow

5.1 Introduction

Lateral connectivity between rivers and their floodplain habitats is essential for the functioning and integrity of floodplain ecosystems (Amoros and Bornette 2002). Several studies have investigated lateral fish movements, especially into floodplain waterbodies and off-channel areas during elevated flows (Sedell *et al.* 1990; Molls and Neumann 1994; Allouche *et al.* 1999), and the importance of backwaters for juvenile (Copp 1997b; Nunn *et al.* 2007a) and adult fish (Hohausová *et al.* 2003). However, little is known about the daily lateral movements of adult and sub-adult fish between such water bodies and the river channel, especially during winter months and under the influence of elevated flow.

In part, this is because current sampling techniques have inherent problems, especially in large rivers. For example, using traps that sampled half the channel width, Hohausová *et al.* (2003) captured only 170 fish moving between a backwater and the River Morava in the Czech Republic. They stated that 'avoidance behaviour could have biased the results' yet still considered the movements to be representative of the population and drew ecological conclusions.

Split-beam hydroacoustic surveys are limited by a low signal-to-noise ratio and a low beam-fit relative to the bed profile and water surface, while conventional underwater cameras are limited by low light levels and high turbidity. A high-definition imaging sonar known as DIDSON (Dual-Frequency Identification Sonar; Sound Metrics Corporation, Washington, US) overcomes some of these limitations because it provides high definition imaging of fish movements when in a fixed location (Moursund *et al.* 2003). Consequently, it may be suitable for *in situ* observation of fish movements and activity in the murky waters of the relatively narrow but deep connection channels between lowland rivers and floodplain waterbodies.

The aim of this study was to determine, using DIDSON, whether movements of fish between the main channel and a backwater in a temperate floodplain river during winter-time vary with time of day and water level. This was achieved by examining movements of fish at the entrance of a marina on the lowland Yorkshire Ouse.

5.2 Materials and methods

5.2.1 Study site

The Yorkshire Ouse in northern England (Figure 5.1), which is described in Chapter 3, is isolated from its floodplain through channelisation and levee construction, except at artificial floodplain features such as marinas. Precipitation run-off from the Pennines often results in elevated river levels, as observed during the sampling period (Figure 5.2), and regular overbank floods. The hydrological responses of the catchment to these floods are perhaps the most important factors stimulating changes in fish distribution (Lucas 2000).

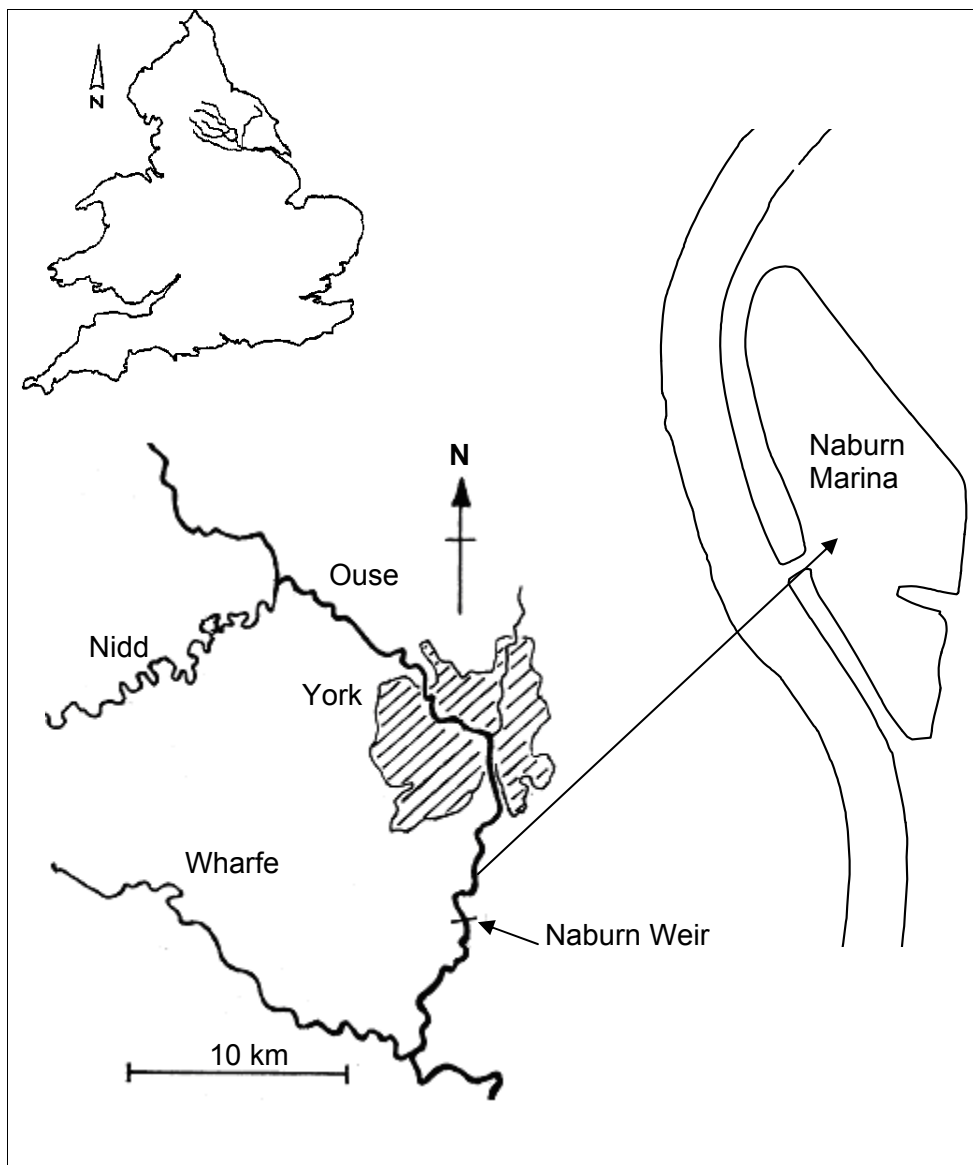


Figure 5.1 Yorkshire Ouse catchment map and Naburn Marina sampling location

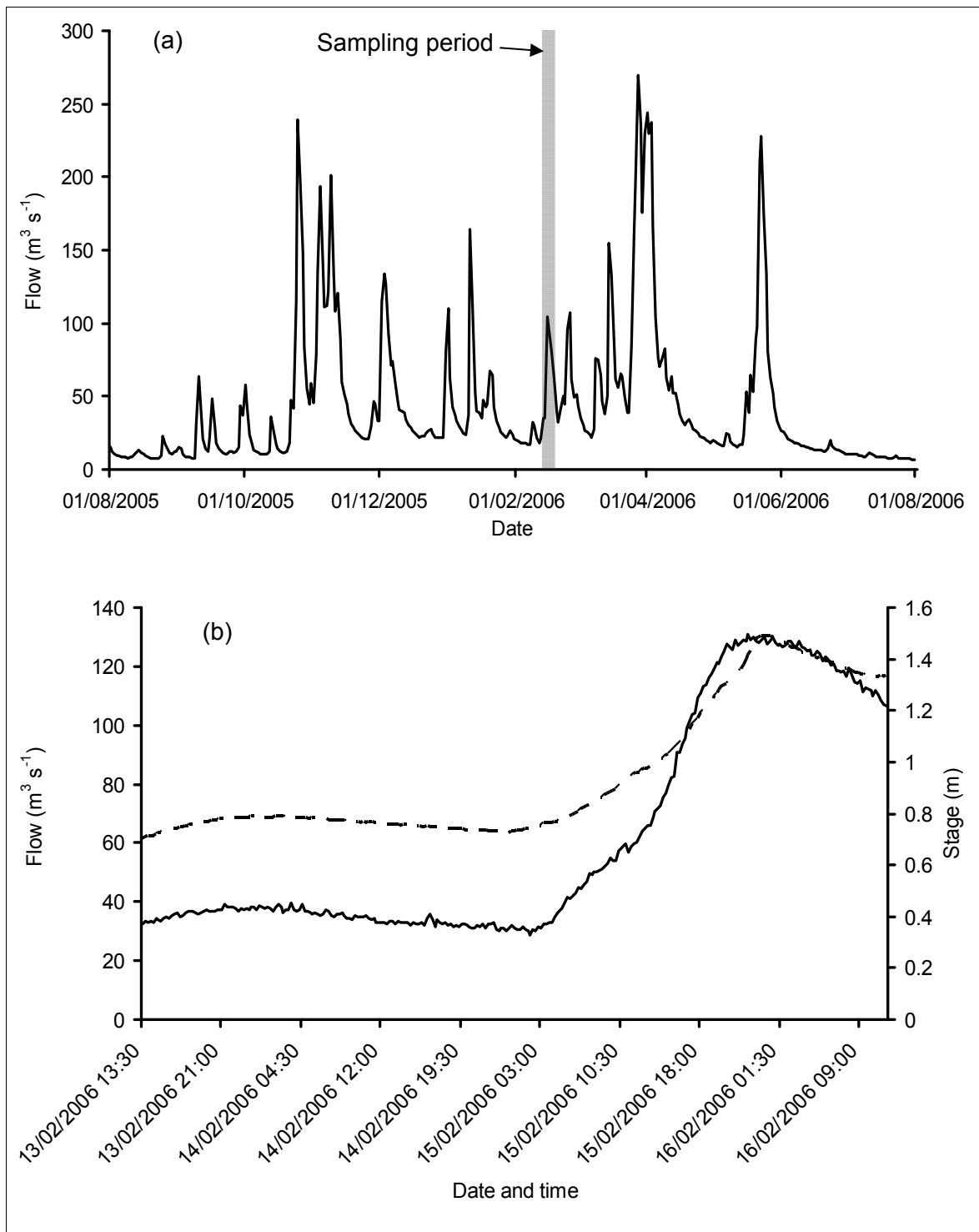


Figure 5.2 Mean daily discharge ($\text{m}^3 \text{s}^{-1}$, complete line) in the Yorkshire Ouse at Skelton from (a) August 2005 to August 2006, and (b) during sampling period (13–16 February 2006) and with river level (m, dashed line)

The deep, slow flowing waters of the lower Ouse are dominated by eurytopic cyprinids and percids, such as roach, bream, bleak, perch, and ruffe (*Gymnocephalus cernuus* (L.)), as well smaller numbers of chub (Whitton and Lucas 1997; Lucas *et al.* 1998).

The study was carried out at Naburn Marina: a backwater feature with an area of 5ha, an average depth of 2m and moorings for about 100 boats during the winter months. It is located approximately 2km upstream of Naburn weir, the tidal limit of the Yorkshire

Ouse. The study was carried out in the connection channel (20m long, 15m wide and 1.75m deep under normal flow) between the river and the marina.

5.2.2 Sampling procedure

A twin-hulled boat was moored on the downstream side of the connection channel inside Naburn Marina on 13–16 February 2006, inclusive. The DIDSON was secured to a 'pan-and-tilt' mechanism mounted on a vertical shaft attached to the front of the boat with the beam directed across the channel entrance. The equipment was mechanically adjusted until the beam produced bottom shadows, giving a sampling reference point during elevated flows, and was subsequently tilted up or down as the water level changed. The boat was able to rise and fall with the increasing and decreasing water level.

River discharge ($\approx 32\text{m}^3\text{ s}^{-1}$) and level ($\approx 0.75\text{m}$) remained stable and close to base level (long term mean discharge $\approx 50\text{m}^3\text{ s}^{-1}$) for the first 37.5 hours of the study, but at 03:00 on 15 February the river began to rise (Figure 5.2). By 18:00 on 15 February, the river level was sufficiently high to sample the upper and lower sections of the water column alternately every 15 minutes. The river reached a maximum flow ($130\text{m}^3\text{ s}^{-1}$) and level (1.49m) at 01:00 on 16 February, equal to a four-fold increase in discharge and an increase in depth of $\approx 0.75\text{m}$. By the end of the sampling period, the flow ($110\text{m}^3\text{ s}^{-1}$) and river level (1.34m) had dropped slightly.

The equipment was operated at high frequency (1.8MHz: 96 beams oriented 0.3° apart, creating a field of view that extended 12° vertically and 29° horizontally), with a 5m field of view that began 4.5m from the DIDSON transponder. Directing fences could not be installed to force fish through the DIDSON beam because these would interfere with boat traffic. Sampling at low frequency mode (1.1MHz) was not employed, despite range benefits, because of the reduced ability to identify small fish. Thus, sampling of the full channel width was not conducted, so as to obtain a more detailed resolution and higher quality data. Continuous observations over a 70-hour period, at a rate of seven frames per second, were recorded onto external hard-drives in 15-minute, date- and time-stamped files.

5.2.3 Output processing

After sampling, the image files (Figure 5.3) generated by the DIDSON were reviewed to estimate fish density in the marina entrance and the direction of fish movements. Data were reduced to a manageable level for analysis by processing the first minute in every five. Files were replayed in image mode and fish were manually counted. Playback speeds and direction were adjusted to help eliminate non-fish targets and so allow the best quality counts of fish targets. A grid and a measuring tool built into the DIDSON software viewing program allowed simple processing of fish numbers and length.

Fish size data were assigned to the following size categories (cm): <15, 15–19, 20–24, 25–29, 30–34, 35–39, 40–44, 45–49, 50–54, 55–59 and >59, but fish lengths were not validated in the field. In high-frequency mode, the generated images showed the outline and fin definition of larger fish. Under certain scenarios, it was possible to identify larger fish, such as large pike and bream, based on differences in morphology (often aided by the acoustic shadow). However, a reliable identification protocol was not available for these species, so fish were not identified to species in this study.

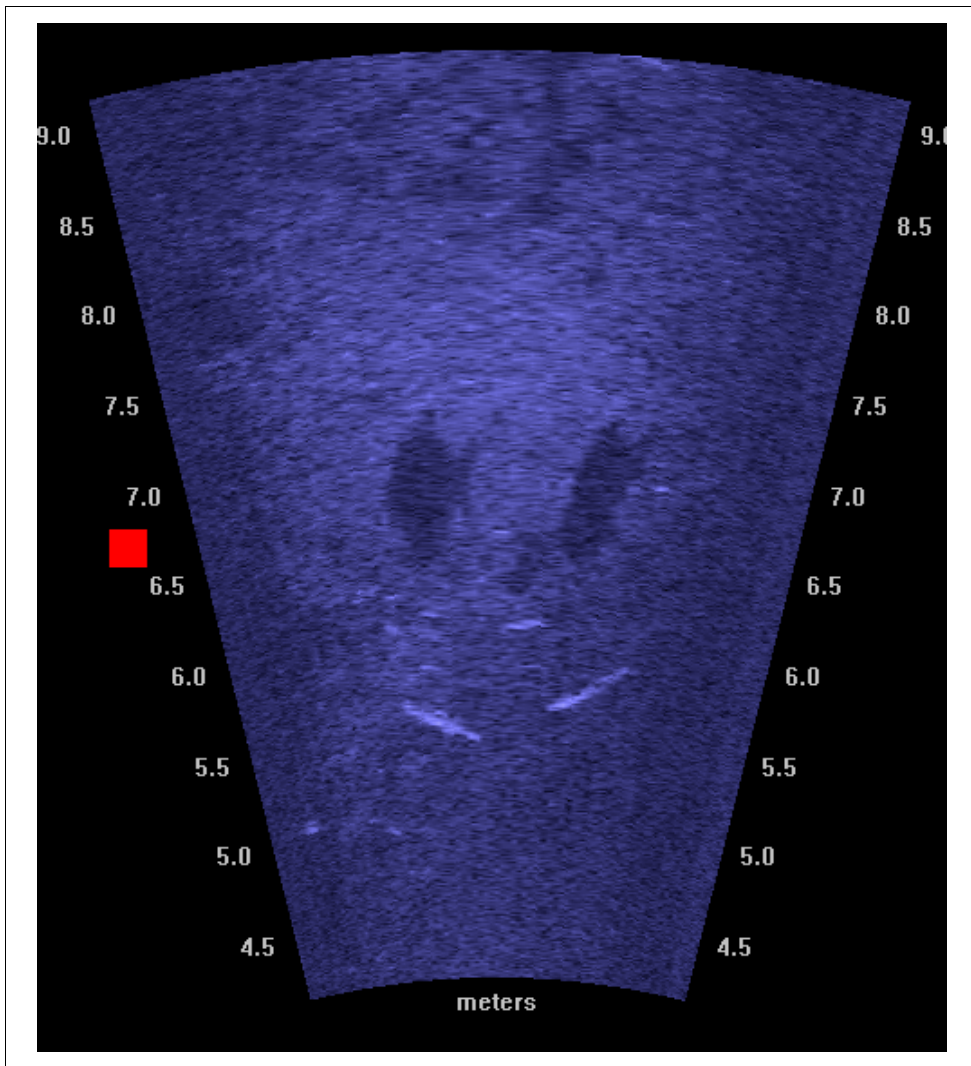


Figure 5.3 Example of a DIDSON image, showing three fish (approximately 20cm, 45cm and 50cm long) between 5.5m and 6.5m from the DIDSON transponder

5.2.4 Data analysis

Fish density (fish m^{-2}) was calculated from the number of fish in the grid either side of the centre line (4° either side, area = $4.9m^2$) at the start of every fifth minute. Fish were considered to be moving either towards or away from the marina when they crossed the centre line of the viewing window, although some 'milling' behaviour occurred. Analysis of Variance (ANOVA) was used to test the null hypothesis that density, movements and size composition of imaged fish did not differ significantly between day and night, or according to the river level (between days 2 and 3 and night 3 compared with nights 1 and 2) or the section of the water column sampled during elevated flow (between days 2 and 3). In addition, daytime (dawn till dusk) was separated into five two-hour periods to allow comparisons both within the same day (dawn to all other sampling periods on day 2) and between days/river level (dawn between days 2 and 3).

The Least Significance Difference (LSD) *post hoc* test was used, except when the variance was not equal (Levene statistic < 0.05), in which case the Games-Howell test was applied. A Mann-Whitney *U*-test was used when two sample groups were compared and the variance was not equal. Comparisons between day sampling periods excluded the first and last days of sampling because of incomplete data sets.

All statistical analysis was carried out using SPSS (version 14.0) with a significance level $\alpha = 0.05$.

5.3 Results

A total of 11,013 fish were counted moving towards Naburn Marina, while 5671 were counted moving away from the marina. Extrapolating counts to include unprocessed minutes (4 in every 5) equates to over 60,000 and 30,000 directional fish movements over the three-day study period. Large variations in fish movements and fish presence in the marina entrance occurred, influenced by time of day, river discharge and position in the water column (Figure 3.4).

The largest and most consistent variations between fish density and movements in the marina entrance were between day and night samples, although other differences were also identified (Tables 5.1–5.3; Figure 3.5). Under normal flow conditions (day 2), density and movements into the marina were similar throughout the day (Games-Howell: all $P > 0.05$), but significantly less fish were imaged leaving the marina at dusk than in the morning ($F_{4,122} = 6.166$, $P < 0.001$).

River levels and flows increased substantially during day 3 and night 3, but no large influx of fish into the marina for refuge was observed. Instead, movements of fish into the marina on day 3 were less than the previous day (Table 5.2). In contrast with day 1 (dusk period only) and day 2, three periods of reduced movements into the marina on day 3 were identified: mid morning (Mann Whitney U-test: $Z = -4.179$, $n = 49$, $P < 0.001$), late afternoon ($F_{1,51} = 16.764$, $P = 0.015$) and dusk ($F_{2,70} = 6.778$, $P = 0.002$). The fish density ($F_{2,70} = 26.719$, $P < 0.001$) and movements away from the marina ($F_{2,70} = 4.134$, $P = 0.020$) were also significantly lower during the period just prior to darkness on day 3 compared with day 1 and day 2.

Significantly fewer fish occupied the upper section of the water column during the raised river levels on night 3 (Mann Whitney U-test: $Z = -5.742$, $n = 155$, $P < 0.001$) and day 3 (Mann Whitney U-test: $Z = -3.818$, $n = 37$, $P < 0.001$) than during the low flows experienced on days 1 and 2. Significantly more fish moved towards the marina close to the surface during the night (Mann Whitney U-test: $Z = -1.976$, $n = 156$, $P = 0.048$), but the opposite was found for fish moving towards the river (ANOVA: $F_{1,155} = 6.032$, $P = 0.015$). During the day, the number of fish moving in both directions was significantly greater near the bottom (Mann Whitney U-test: towards - $Z = -4.013$, $n = 37$, $P < 0.001$; ANOVA: away from - $F_{1,36} = 13.036$, $P = 0.001$).

The size composition of imaged fish was highly variable throughout the sampling period (Table 5.1). This was due to the mixed species and size groups of mainly cyprinid fishes prevalent in the river, which limited analysis of size class results. However, on the last night, during elevated river levels, significantly greater density ($F_{4,635} = 21.137$, $P < 0.001$) and movements of $>30\text{cm}$ fish were observed than during all other sampling periods (towards: $F_{4,635} = 15.198$, $P < 0.001$; away from: $F_{4,635} = 17.622$, $P < 0.001$) (Tables 5.1–5.3). Although no species identification protocol was developed for this study, the fish were considered to be bream because of body shape characteristics evident on the DIDSON images.

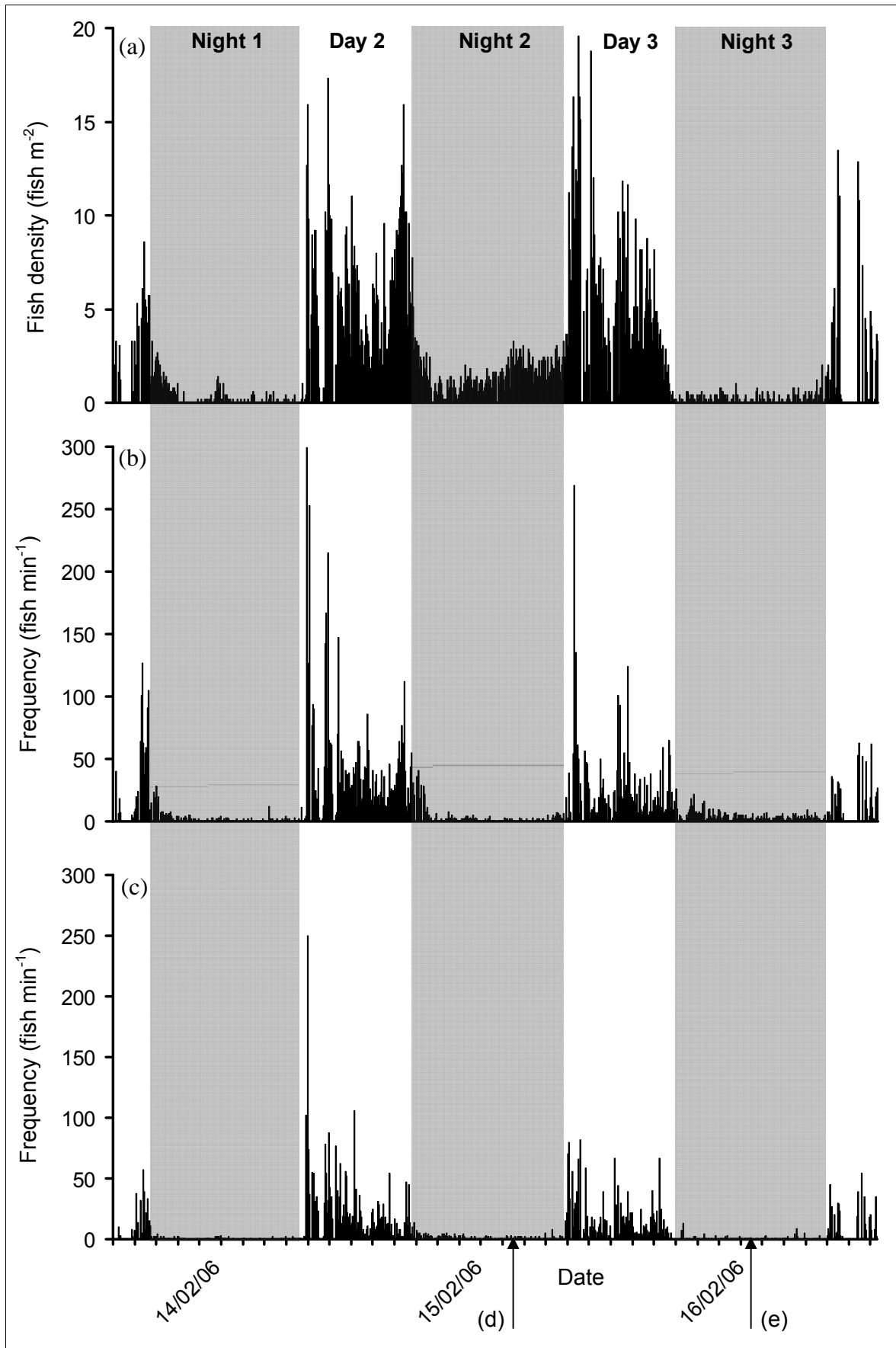


Figure 5.4 (a) Fish density (fish m^{-2}) and movements (per minute) (b) towards and (c) away from the marina throughout the study period

Note: Shaded area represents night and (d) and (e) correspond to start and peak of elevated flow.

Table 5.1 Mean density (fish m⁻² ± SD (%)) at start of each minute processed (n, no. of fish (%)) during day and night sampling periods for all length classes (cm)

Size class (cm)	Day 1	Night 1	Day 2	Night 2	Day 3	Night 3, bottom	Night 3, surface	Day 4, bottom	Day 4, surface
<15	2.66 ± 1.94 (93.1)	0.21 ± 0.37 (89.1)	4.99 ± 3.25 (88.5)	1.27 ± 0.63 (87.4)	4.69 ± 3.84 (92.3)	0.10 ± 0.18 (24.8)	0.07 ± 0.14 (53.1)	4.86 ± 3.34 (88.1)	1.77 ± 3.33 (94.6)
15–19	0.15 ± 0.27 (5.2)	0.01 ± 0.06 (4.9)	0.61 ± 1.08 (10.9)	0.17 ± 0.26 (11.9)	0.36 ± 0.38 (7.1)	0.10 ± 0.15 (26.9)	0.04 ± 0.09 (32.7)	0.49 ± 0.40 (8.9)	0.06 ± 0.16 (3.5)
20–24	0.03 ± 0.09 (1.2)	0.01 ± 0.04 (2.2)	0.02 ± 0.08 (0.4)	0	0.02 ± 0.06 (0.3)	0.10 ± 0.13 (24.8)	0.01 ± 0.05 (8.2)	0.08 ± 0.13 (1.5)	0.02 ± 0.06 (1.0)
25–29	0.01 ± 0.30 (0.2)		0.00 ± 0.02 (0.0)		0.00 ± 0.03 (0.1)	0.01 ± 0.03 (1.4)	0.00 ± 0.02 (2.0)		
30–34	0	0.00 ± 0.02 (0.6)	0	0.00 ± 0.02 (0.1)	0.00 ± 0.02 (0.0)	0	0	0.01 ± 0.05 (0.3)	0.01 ± 0.04 (0.5)
35–39	0	0.00 ± 0.02 (0.6)	0	0	0	0.01 ± 0.05 (2.76)	0	0.01 ± 0.05 (0.3)	0
40–44	0	0.00 ± 0.03 (1.64)	0.00 ± 0.04 (0.1)	0.00 ± 0.02 (0.2)	0.00 ± 0.02 (0.0)	0.01 ± 0.05 (2.8)	0	0.03 ± 0.07 (0.5)	0
45–49	0.01 ± 0.03 (0.2)	0	0.00 ± 0.02 (0.0)	0.00 ± 0.02 (0.2)	0.00 ± 0.03 (0.1)	0.04 ± 0.08 (9.7)	0	0.03 ± 0.07 (0.5)	0
50–54	0	0.00 ± 0.02 (0.6)	0.00 ± 0.03 (0.1)	0.00 ± 0.02 (0.2)	0.00 ± 0.03 (0.1)	0.01 ± 0.05 (2.76)	0.01 ± 0.03 (4.1)	0	0.01 ± 0.04 (0.5)
55–59	0	0.00 ± 0.02 (0.6)	0	0	0	0.00 ± 0.02 (0.7)	0	0	0
>59	0.01 ± 0.03 (0.2)	0	0	0.00 ± 0.02 (0.1)	0.00 ± 0.03 (0.1)	0.01 ± 0.05 (3.5)	0	0	0
All	2.86 ± 2.03	0.23 ± 0.39*	5.64 ± 3.50 ^a	1.46 ± 0.77	5.09 ± 4.08 ^a	0.39 ± 0.35*	0.13 ± 0.19	5.51 ± 3.51	1.87 ± 3.45

Note: Sampling periods (from night 1 to night 3, bottom) sharing the common subscript (a) are not significantly different, whereas the other comparisons differ at $P < 0.001$, except where $P < 0.05$ (denoted by *) for both sampling periods.

Table 5.2 Mean (\pm SD (%)) number of fish moving towards the marina per minute during day and night sampling periods for all length classes (cm)

Size class (cm)	Day 1	Night 1	Day 2	Night 2	Day 3	Night 3, bottom	Night 3, surface	Day 4, bottom	Day 4, surface
<15	25.9 \pm 31.4 (90.3)	1.2 \pm 1.9 (74.7)	30.8 \pm 30.2 (74.3)	1.6 \pm 2.3 (78.0)	20.2 \pm 28.8 (84.3)	0.9 \pm 1.3 (31.8)	2.6 \pm 3.4 (55.2)	25.2 \pm 18.1 (82.0)	5.7 \pm 7.5 (73.9)
15–19	2.5 \pm 3.4 (8.7)	0.3 \pm 0.5 (16.3)	9.9 \pm 19.8 (23.9)	0.3 \pm 1.1 (15.2)	3.5 \pm 4.8 (14.5)	1.2 \pm 1.1 (40.7)	1.8 \pm 1.7 (37.7)	4.4 \pm 2.9 (14.1)	1.8 \pm 2.8 (22.9)
20–24	0.1 \pm 0.3 (0.3)	0.1 \pm 0.2 (3.3)	0.7 \pm 1.3 (1.6)	0.0 \pm 0.2 (1.2)	0.2 \pm 0.7 (0.9)	0.3 \pm 0.5 (11.7)	0.2 \pm 0.5 (4.3)	0.4 \pm 0.6 (1.3)	0.2 \pm 0.4 (2.0)
25–29	0.1 \pm 0.3 (0.3)	0.0 \pm 0.1 (0.8)	0	0.0 \pm 0.1 (0.3)	0.0 \pm 0.1 (0.0)	0.0 \pm 0.1 (0.5)	0.0 \pm 0.2 (0.8)	0.4 \pm 0.7 (1.3)	0
30–34	0	0	0.0 \pm 0.2 (0.1)	0	0	0.0 \pm 0.2 (1.4)	0.0 \pm 0.2 (0.8)	0	0
35–39	0.0 \pm 0.2 (0.1)	0.0 \pm 0.2 (1.6)	0.0 \pm 0.1 (0.0)	0.0 \pm 0.1 (0.3)	0	0.1 \pm 0.3 (2.3)	0	0.1 \pm 0.2 (0.2)	0
40–44	0	0.0 \pm 0.1 (0.8)	0.0 \pm 0.1 (0.0)	0.0 \pm 0.1 (0.3)	0.0 \pm 0.2 (0.1)	0.1 \pm 0.3 (3.7)	0.0 \pm 0.2 (0.5)	0.1 \pm 0.2 (0.2)	0.1 \pm 0.2 (0.7)
45–49	0.1 \pm 0.3 (0.3)	0	0.0 \pm 0.1 (0.0)	0.1 \pm 0.3 (3.1)	0.0 \pm 0.2 (0.2)	0.2 \pm 0.4 (5.6)	0.0 \pm 0.2 (0.5)	0.1 \pm 0.2 (0.2)	0
50–54	0	0.0 \pm 0.2 (2.0)	0.0 \pm 0.1 (0.0)	0.0 \pm 0.2 (1.2)	0.0 \pm 0.1 (0.0)	0.0 \pm 0.2 (1.4)	0	0.1 \pm 0.3 (0.4)	0.1 \pm 0.2 (0.7)
55–59	0	0	0	0	0.0 \pm 0.1 (0.0)	0.0 \pm 0.2 (0.9)	0	0.1 \pm 0.2 (0.2)	0
>59	0	0.0 \pm 0.1 (0.4)	0.0 \pm 0.1 (0.0)	0.0 \pm 0.1 (0.3)	0.0 \pm 0.1 (0.0)	0	0.0 \pm 0.1 (0.3)	0	0
All	28.6 \pm 33.3	1.5 \pm 2.0 ^a	41.4 \pm 45.3*	2.1 \pm 3.2 ^{ab}	23.9 \pm 31.9*	3.0 \pm 2.0 ^b	4.8 \pm 4.3	30.8 \pm 18.9	7.7 \pm 9.9

Note: Sampling periods (from night 1 to night 3, bottom) sharing the common subscript (a, b) are not significantly different, whereas the other comparisons differ at $P < 0.001$, except where $P < 0.05$ (denoted by *) for both sampling periods.

Table 5.3 Mean (\pm SD, (%)) number of fish moving away from the marina per minute, during day and night sampling periods for all length classes (cm)

Size class (cm)	Day 1	Night 1	Day 2	Night 2	Day 3	Night 3, bottom	Night 3, surface	Day 4, bottom	Day 4, surface
<15	8.4 \pm 12.2 (85.2)	0.3 \pm 0.5 (64.2)	16.7 \pm 23.9 (76.4)	1.0 \pm 1.2 (78.6)	11.2 \pm 14.1 (79.9)	0.2 \pm 0.5 (21.0)	0.2 \pm 0.6 (41.7)	18.1 \pm 12.6 (84.1)	5.6 \pm 11.1 (91.1)
15–19	1.3 \pm 2.2 (12.9)	0.0 \pm 0.2 (10.4)	4.8 \pm 8.8 (22.1)	0.2 \pm 0.4 (13.5)	2.6 \pm 4.6 (18.5)	0.1 \pm 0.3 (9.7)	0.1 \pm 0.5 (27.8)	1.6 \pm 1.7 (7.7)	0.6 \pm 1.3 (8.9)
20–24	0.2 \pm 0.4 (1.7)	0.0 \pm 0.2 (6.0)	0.3 \pm 0.7 (1.2)	0	0.1 \pm 0.5 (0.9)	0.1 \pm 0.3 (8.1)	0.0 \pm 0.2 (5.6)	0.4 \pm 0.6 (1.9)	0
25–29	0.0 \pm 0.2 (0.3)	0	0	0.0 \pm 0.1 (0.5)	0.0 \pm 0.1 (0.1)	10.0 \pm 0.1 (1.6)	0.0 \pm 0.2 (8.3)	0.4 \pm 0.6 (1.6)	0
30–34	0	0.0 \pm 0.1 (1.5)	0.0 \pm 0.1 (0.1)	0	0.0 \pm 0.1 (0.1)	0	0	0.2 \pm 0.5 (0.8)	0
35–39	0	0	0	0	0.0 \pm 0.1 (0.1)	0.0 \pm 0.1 (1.6)	0	0.1 \pm 0.2 (0.3)	0
40–44	0	0.0 \pm 0.1 (4.5)	0.0 \pm 0.1 (0.1)	0.0 \pm 0.1 (1.6)	0.0 \pm 0.1 (0.1)	0.1 \pm 0.4 (12.9)	0.0 \pm 0.2 (5.6)	0.1 \pm 0.3 (0.5)	0
45–49	0	0.0 \pm 0.1 (4.5)	0	0.0 \pm 0.2 (3.6)	0.0 \pm 0.1 (0.1)	0.2 \pm 0.5 (27.4)	0	0.3 \pm 0.5 (1.4)	0
50–54	0	0.0 \pm 0.2 (6.0)	0	0.0 \pm 0.2 (2.1)	0	0.1 \pm 0.3 (9.7)	0.0 \pm 0.2 (5.6)	0.3 \pm 0.6 (1.4)	0
55–59	0	0.0 \pm 0.1 (1.5)	0	0	0.0 \pm 0.1 (0.1)	0.0 \pm 0.2 (4.8)	0.0 \pm 0.2 (5.6)	0.1 \pm 0.2 (0.3)	0
>59	0	0.0 \pm 0.1 (1.5)	0.0 \pm 0.2 (0.1)	0	0.0 \pm 0.1 (0.1)	0.0 \pm 0.2 (3.2)	0	0	0
Total	9.9 \pm 13.8	0.4 \pm 0.7*	21.8 \pm 29.9 ^a	1.2 \pm 1.3 ^b	14.0 \pm 17.5 ^a	0.9 \pm 1.1* ^b	0.4 \pm 1.1	21.5 \pm 13.8	6.2 \pm 12.0

Note: Sampling periods (from night 1 to night 3, bottom) sharing the common subscript (a, b) are not significantly different, whereas the other comparisons differ at $P < 0.001$, except where $P < 0.05$ (denoted by *) for both sampling periods.

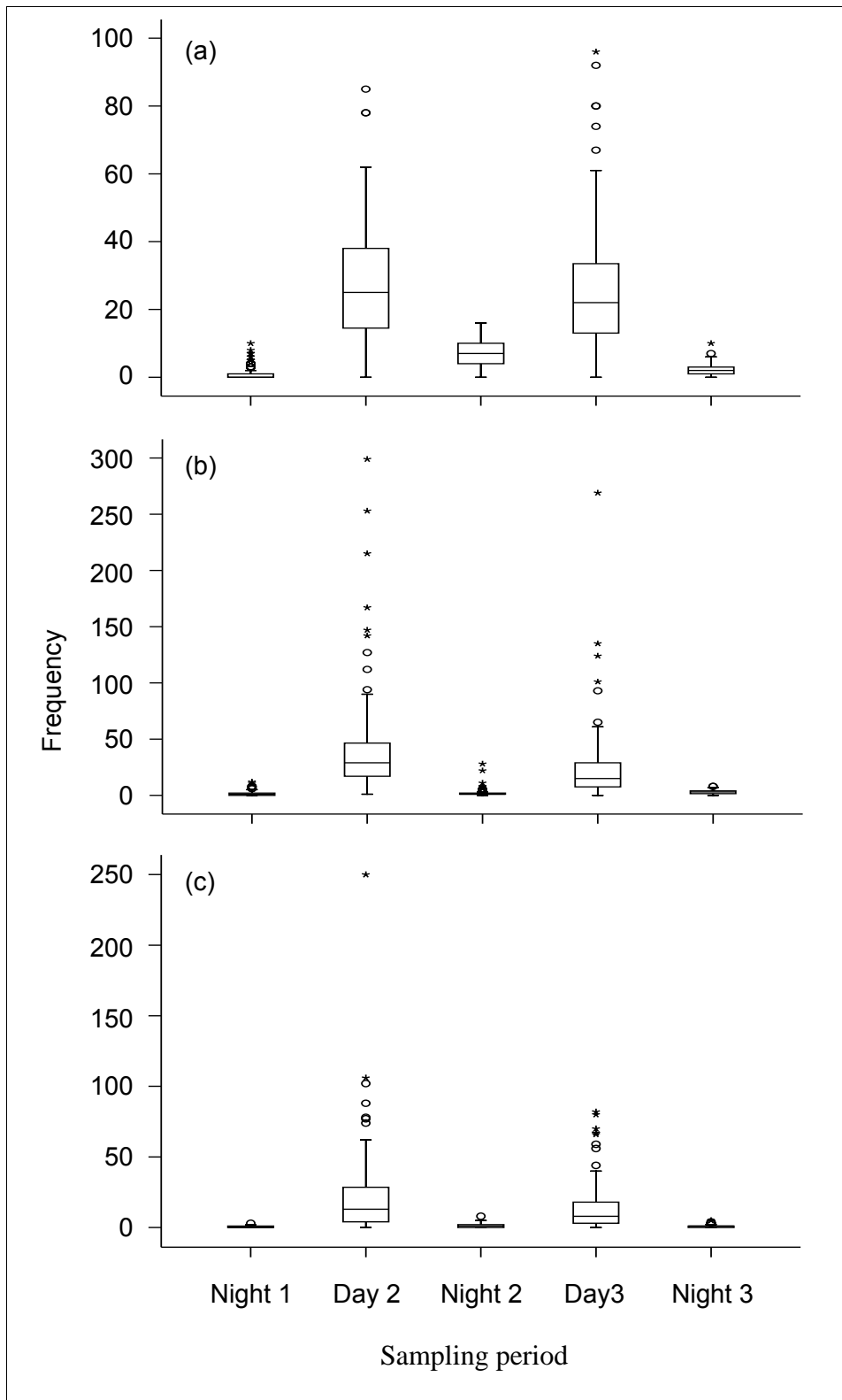


Figure 5.5 Box plots (10th, 25th, 50th, 75th and 90th percentiles and symbols = outliers) for (a) fish density (fish in sampled area; 4.9m²) and movements (per minute) (b) towards and (c) away from the marina throughout the study period

5.4 Discussion

DIDSON offers a valuable, non-intrusive, high-resolution tool for studying patterns of individual fish movements between river channels and backwaters. Using DIDSON, it was found that fish movements were generally towards the marina during the study period. However, large scale diel variations in fish density and movements were also found between the river and the marina backwater, influenced by river flow and fish size. The processes that influence fish distribution are rarely random (Huntingford 1993). It is therefore necessary to consider the variations in the movement and activity of cyprinids and percids in terms of processes such as foraging, predator avoidance trade-offs and the influence of flow on energy expenditure.

Despite the potential mosaic of movements by different species, DIDSON identified diurnal (principally around dawn) peaks in fish density and activity, with the lowest presence and movement levels at night. Alabaster and Robertson (1961) found that roach, bream and perch activity increased at dusk and dawn, with perch and bream shoals breaking up at night. For most fishes, diel behaviour is often separated into active periods of foraging and passive periods of resting, linked to predator avoidance (Werner *et al.* 1983; Helfman 1993). However, during winter, food supplies are scarce and feeding rates are low (van Dijk *et al.* 2005). Thus, fish may use backwaters to minimise energetic costs, with diel movements reflecting the risk of predation from birds (Gliwicz and Jachner 1992; Jepsen and Berg 2002; Heermann and Borcharding 2006).

Numerous piscivorous birds, including the cormorant (*Phalacrocorax carbo* (L.)), overwinter on the lower Ouse close to the study location (Whitton and Lucas 1997) and have been observed feeding in the river adjacent to the marina, although human activity in the marina may make it a safer environment for fish. Nevertheless, even low numbers of birds feeding on the river could pose a sufficient threat to induce habitat shifts. This is because of the cumulative probability of an encounter (Gliwicz *et al.* 2006), combined with the daily food requirements of warm-blooded predators during winter months (Gremillet *et al.* 2003).

During the night, habitat usage altered (as shown by the significant drop in the number of fish observed in the marina entrance) and behaviour changed, since significantly fewer fish were imaged moving between the river and the marina. Bi-directional movements of fish at dusk suggest they moved both into the marina and into the river. Ultimately, fish dispersed to areas outside of the area visualised by the DIDSON, making any interpretation of activity and habitat use somewhat limited.

During river level rises, fish may be attracted to low flow areas because they are energetically less demanding than trying to maintain a position in the potentially faster flowing water of the main channel (Gillette *et al.* 2006). However, significantly fewer fish moved towards Naburn Marina during the elevated flow event that occurred during the present study. This finding was contrary to reported fish movements into floodplain waterbodies (Sedell *et al.* 1990; Molls and Neumann 1994) and off-channel areas (Allouche *et al.* 1999) for refuge during floods.

There are a number of possible explanations for this finding. First, habitat complexity within the river or inundated terrestrial vegetation may have provided sufficient localised refuge from elevated flows (Pearsons *et al.* 1992; Schwartz and Herricks 2005). Lucas *et al.* (1998) reported that echo-counted fish densities were three times lower during high flows, suggesting that fish remained on the river bottom or in the margins to avoid higher velocities in the water column. Second, conditions in the river may not have been sufficiently severe to cause such movements. During winter, the Yorkshire Ouse regularly reaches flows observed during the study, thus fish in the river are probably capable of living in this kind of regularly fluctuating environment. Third,

fish were moving into the marina as monitoring started in response to weather patterns that anticipated high flows, but continued to make localised feeding forays except during the period of highest flows. However, this latter explanation is unlikely, because rain fell on the upper part of the catchment rather than at the sampling location.

During the elevated flow, fish believed to be large bream were imaged in the marina channel, but only at night. Rakowitz and Zweimuller (2001) found fish >400mm in total length tended to move upstream during increasing discharge levels. Lyons and Lucas (2002), Borcharding *et al.* (2002) and Schulz and Berg (1987) documented diel feeding migrations by bream, suggesting that foraging requirements provide the stimulus for the observed diel behaviour.

Although the study was of limited duration, did not sample the full width of the channel and could not ascertain the extent of 'milling' behaviour, the experimental design was comparable to similar studies employing split-beam hydroacoustic technology (Rakowitz and Zweimuller 2001; Lilja *et al.* 2003). Additionally, these limitations were considered necessary to obtain detailed, high resolution information. However, such experimental decisions possibly generated unexpected results. For example, the net movement of fish into the marina during the study period could be attributed to lunar cycles (Gaudreau and Boisclair 2000), temperature (Lilja *et al.* 2003) or turbidity variations beyond the timescale of this study (Jepsen and Berg 2002).

This study demonstrated the usefulness of the DIDSON in providing a fine-resolution insight into the movements of fish between a lowland river and a connected floodplain waterbody during winter months. In particular, temporal changes in the density, activity and size distribution of the fish suggest connected floodplain waterbodies serve as essential winter habitat and are important for river ecosystem functioning.

The findings of this study and other investigations involving backwater use in winter months should be explicitly incorporated into plans for lowland river rehabilitation and floodplain restoration (Cowx and Welcomme 1998), including actions to improve the ecological status of rivers under the WFD. From a conservation perspective, it is important to note that these patterns may be applicable on an assemblage-wide level rather than just a species-specific level.

Future investigations should attempt to verify the numbers, species and size composition of imaged fish over multiple 24-hour periods. They should also be over an extended period and area, and should measure detailed water quality variables (suspended solids, ammonia) in the marina and the river. There is also a need to gather data throughout the year to describe seasonal patterns in marina use.

6 Evaluation of visible implant elastomer marking and passive integrated transponder tagging protocols for juvenile cyprinid fishes

6.1 Introduction

One of the primary actions taken in response to the poor performance of fisheries or to compensate for loss of fish caused by mortality or environmental degradation is stocking (Cowx 1994). The efficacy of these stocking events is usually unknown (Cowx 1999) and so a better understanding of the fate of stocked fish is needed to improve their effectiveness. This generally involves some form of marking to identify fish either individually or as part of a group. Marking animals for identification is also of fundamental importance in assessing population size, movement, growth, age and fecundity (Wydoski and Emery 1983).

In general, marking techniques (including tags) should: (1) identify individual fish or batches; (2) not affect the growth, survival, behaviour or capture probability of marked individuals; (3) be retained for the duration of the study; (4) be easily applied and identified; and (5) be inexpensive (Kelly 1967; Wydoski and Emery 1983; McFarlane *et al.* 1990). Studies that require such characteristics necessarily limit the type of mark that can be used (Lucas and Baras 2000), with the choice of mark further limited when considering juveniles (Thedinga *et al.* 1997).

Visible implant elastomer (VIE; Northwest Marine Technology, Shaw Island, Washington, US) is a biologically inert, brightly coloured, fluorescent polymer that is externally visible after being injected subcutaneously under transparent or semi-opaque tissue. VIE is commonly used as a batch mark in mark-recapture fisheries studies using multiple combinations of locations and VIE colours (Bonneau *et al.* 1995; Olsen and Vollestad 2001; Walsh and Winkelman 2004).

A disadvantage of VIE marking is that it is more suitable for group marking than individual identification (Woods and James 2003), although small ecological studies have used VIE to mark individuals (for example, Dewey and Zigler 1996; Brennan *et al.* 2005). The only study in which cyprinid fishes have been VIE marked involved barbel, where high retention rates were found after 57 days when the barbel were marked in the head and fins (Farooqi and Morgan 1996). However, other studies that implanted VIE in the head and fins found variable retention (Dewey and Zigler 1996; Brennan *et al.* 2005), emphasising the need to validate VIE marking for the specific species under study.

Passive integrated transponder (PIT) tags are biocompatible, sealed, electronic modules that return a unique identification number when probed by an external antenna (Gibbons and Andrews 2004). PIT tags theoretically have an indefinite life

span and allow repeated, non-destructive sampling or direct telemetric data transmission. They have proven useful for monitoring individual fish movements, migrations and habitat use (Prentice *et al.* 1990a, b; Castro-Santos *et al.* 1996; Armstrong *et al.* 1996; Ombredane *et al.* 1998; Lucas *et al.* 1999; Roussel *et al.* 2000; Zydlewski *et al.* 2001; Riley *et al.* 2003).

Many PIT systems use 12mm tags, which despite their small detection range (<0.4m) can be used to tag fish as small as 6cm and are ideal for mark-recapture and some telemetry applications (Lucas and Baras 2000). Larger PIT tags (such as 23mm) have a greater range and this enhances their utility for certain telemetry applications, but there is a trade-off in terms of the potential impact on the health of smaller fishes (Roussel *et al.* 2000; Lucas and Baras 2000). Many telemetry studies have recommended that the tag weight should not exceed 2% of the fish body mass (for example, Winter 1996; Adams *et al.* 1998), because of the adjustment capacity of the swimbladder in teleost fish (Alexander 1966). Ultimately, proportionally smaller tags are likely to have less damaging effects on fish released into the wild.

All methods of marking fish (of which tags are a subset) have the potential to influence fish survival, performance (growth) and behaviour, with the exception of certain natural marks (such as genetic marks) (Lucas and Baras 2000). As a result, feasibility studies on mark suitability are strongly encouraged, for both ethical considerations and validation of results (Baras *et al.* 2000). This is because for ecological experiments to be meaningful marked fish should be representative of unmarked populations (Malone *et al.* 1999). Therefore, before incorporating marking techniques into field research, mark retention and the survival and growth rate of marked fish, along with ease of application and detectability, should be evaluated for each marking technique, fish species, attachment location and size of fish (Guy *et al.* 1996).

Although there have been numerous studies conducted on mark retention, and the mortality and growth rates of fishes, especially salmonids, marked with VIE or PIT tags, few have considered their suitability for cyprinids (Farooqi and Morgan 1996; Skov *et al.* 2005). This study tested the performance of VIE marks and PIT tags and their effects on juvenile chub, dace and roach. The overall objective was to determine the most reliable and appropriate long-term marking technique for potential application in field studies assessing dispersal of juvenile cyprinids.

6.2 Materials and methods

6.2.1 Fish origin and experimental setup

All fish were artificially reared in the hatchery and pond facility of the Environment Agency's Calverton Fish Farm in Nottinghamshire, England, which was also the site of the experimental work. Fish marked in this experiment covered the range of ages and sizes usually stocked into UK rivers in order to ensure the results were applicable to future field studies on marked stock fish. In April 2004, approximately 400 fish of each of the following species groups were brought into indoor tanks (2.02m³) supplied (in parallel) with filtered ground water (60L⁻¹ min⁻¹ tank⁻¹): chub (87–167mm fork length, Lt), dace (77–152mm, Lt), roach (103–150mm, Lt) and larger chub (114–210mm, Lt).

Fish were acclimated to the experimental environment for one month prior to marking. Water temperature (range 17–21°C) and dissolved oxygen (>90% saturation throughout) were monitored and the photoperiod was controlled to simulate the daily cycle. Fish were fed a ration of approximately 3% body mass per day using automatic feeders, supplemented by natural frozen gamma-radiated feed.

Treatments (Table 6.1) were tested on groups of 100 fish per tank for large chub and 240 small fish per tank (comprising 80 each of small chub, dace and roach). Limited availability of tanks (nine) required the small fish to be held as mixed species rather than separately. It also prevented treatment replication, although the fish were on exactly the same water and feed delivery systems and housed in the same building to minimise any possible variation.

Table 6.1 Summary of treatment, species of fish, initial sizes (mm, g) and ratio (%) of PIT tag weight to initial fish mass for each treatment

Treatment applied	Species group	Fish length (mean (range), mm)	Fish mass (mean (range), g)	Tag / body wt ratio (mean (range), %)
Control	Large chub	164.9 (114–210)	56.6 (18.3–113.9)	-
VIE (head + fin)	Large chub	140.4 (123–164)	35.3 (23.7–55.4)	-
23mm PIT, no closure	Large chub	167.3 (136–192)	58.1 (29.4–89.0)	1.03 (0.67–2.04)
23mm PIT, with closure	Large chub	169.4 (141–210)	60.7 (37.3–112.7)	0.99 (0.53–1.61)
Control	Small chub	122.2 (88–158)	22.8 (8.4–48.7)	-
	Dace	116.5 (99–143)	16.4 (10.6–30.4)	-
	Roach	118.1 (103–136)	22.8 (15.1–33.9)	-
VIE (head + fin)	Small chub	120.8 (100–157)	20.9 (11.1–46.6)	-
	Dace	116.6 (101–152)	16.0 (10.7–39.0)	-
	Roach	120.4 (104–140)	34.1 (15.6–42.0)	-
Sham	Small chub	117.7 (91–167)	19.1 (8.3–32.2)	-
12mm PIT	Dace	115.7 (101–129)	15.6 (9.7–25.3)	-
	Roach	117.7 (104–134)	21.9 (15.1–34.3)	-
12mm PIT, no closure	Small chub	113.2 (87–126)	16.8 (7.0–24.1)	0.59 (0.41–1.43)
	Dace	114.7 (101–121)	15.3 (10.9–21.2)	0.64 (0.47–0.92)
	Roach	116.3 (104–133)	21.2 (14.6–34.8)	0.47 (0.29–0.68)
23mm PIT, with closure	Small chub	124.7 (110–153)	22.9 (14.6–43.3)	2.62 (1.39–4.11)
	Dace	120.5 (108–140)	17.5 (11.1–30.1)	3.42 (1.99–5.41)
	Roach	122.6 (109–150)	24.7 (16.2–45.9)	2.43 (1.31–3.70)

6.2.2 Marking procedure

The fish were lightly anaesthetised with buffered tricaine methane-sulphonate (MS-222, 0.1 g L⁻¹) before handling and marking. Initial body mass (Wt, g) and fork length (mm) were recorded (Table 6.1). The fish were placed ventral side up in a clean V-shaped foam support soaked in water deep enough to submerge their gills.

VIE treatment procedures for both size classes involved marking the head (subcutaneously, over the cranium) and a fin (between fin rays) with a single ≈2mm fluorescent orange, elastomer mark (Northwest Marine Technology, Shaw Island, Washington, US), using a 1mL syringe and a 27-gauge x 12mm long needle. VIE was applied to one of the paired fins, normally a pectoral fin. However, when this proved difficult, especially in small fish, it was instead applied to a pelvic fin. The elastomer was injected as the needle was withdrawn, stopping before the needle bevel reached the entry point, and a thumb was then gently wiped over the wound to remove any excess elastomer (Olsen and Vollestad 2001).

Tagging fish with a 12mm PIT tag involved inserting an alcohol-sterilised and distilled water-rinsed UKID transponder (model 122GL, 12.0mm long x 2.1mm diameter, 0.1g weight in air, 125kHz, full-duplex; E. Collinson and Co Ltd, Preston, UK) into the body

cavity through an approximately 3mm long ventro-lateral incision made with a scalpel, 2–3 mm anterior to the muscle bed of the pelvic fins. No closure was required because of the small size of the incision. The sham incision treatment involved conducting the same experimental and surgical procedure but without inserting the transponder into the fish.

The 23mm PIT tag treatment was tested on the small chub, dace and roach (with adhesive closure) and the large chub (with and without adhesive closure). The 23mm tags used were half-duplex transponders (Texas Instruments model RI-TRP-RRHP, 23.0mm long x 3.4mm diameter, 0.6g weight in air, 134.2kHz; RFID Components Ltd, Bedford, UK). Each tag was sterilised in alcohol and rinsed with distilled water before being inserted into the body cavity through an approximately 5mm long ventro-lateral incision made with a scalpel, 4–6mm anterior to the muscle bed of the pelvic fins.

In one group of large chub tagged with 23mm PITs, the incision was not closed. In the other large chub treatment group and for all small chub, dace and roach tagged with 23mm PITs, clinical grade cyanoacrylate adhesive (Vetbond, 3M) was applied to the periphery of the incision and gentle pressure applied for five seconds to close the wound. A large range of PIT tag weight/body mass ratios was achieved by using different-sized PIT tags and fish (Table 6.1).

Control fish were weighed, measured and handled using the same protocol as the fish in the other treatments, but no surgery was performed or tags implanted. After treatment, the fish were allowed to recover from the anaesthetic in a well-aerated observation tank until they regained their balance and were observed actively swimming, after which they were returned to the experimental tanks.

All fish were treated in compliance with the UK Animals (Scientific Procedures) Act 1986; Home Office licence number PPL 60/3260.

6.2.3 Monitoring procedure

Tanks were inspected daily for mortalities (with any dead fish removed and frozen, and the tank number of origin recorded) and signs of disease throughout the experiment. All fish were examined after 29 days (1 month), 89 days (3 months) and 182 days (6 months) to determine mark retention, wound healing and growth over short and long timescales. On each occasion, the fish were anaesthetised with MS-222, and their fork length (mm) and mass (g) recorded to assess growth. The fish (and the tank bottom) were screened for PIT tag presence and function using a Trovan LID 500 hand detector (Trovan Ltd, Douglas, UK) for 12mm tags and an Allflex compact reader P/N 930009-001 (Allflex, Hawick, UK) for 23mm tags.

Identification of fluorescent VIE marks was conducted using a Northwest Marine Technology, 7-LED 'blue' flashlight and amber lens spectacles. Despite fragmentation and partial losses of VIE in both mark locations, marks were still considered to be retained if any fragment was visible, since this is a useful field assessment condition. The condition of the marking site was examined and assigned to one of four classes: 0 = fully healed (no scar visible); 1 = visible wound but no reddening; 2 = slight inflammation (slight reddening around the incision sight); and 3 = strong inflammation (marked reddening around the incision site). For consistency, the same person performed the visual inspection throughout the entire experiment. After inspection, fish were allowed to recover from the anaesthetic in a well-aerated observation tank until they recovered their balance and were observed actively swimming, after which they were returned to the experimental tanks.

6.2.4 Data analysis

Mark retention was expressed as a percentage of the total number of marks implanted. A chi-squared test with continuity correction was used to test the null hypothesis that mark retention did not differ significantly between marking technique and locations. Mortality rate was calculated as a cumulative percentage of dead fish per treatment for each species during the experiment. A chi-squared test was used to test the null hypothesis that survival did not differ significantly between marking techniques, followed by a Mann-Whitney *U*-test, as a *post hoc* test, to determine mortality rates in treatment groups that were significantly different from control fish. A *t*-test was performed on the initial length and mass of surviving fish and dead PIT-tagged fish to test the null hypothesis that fish size had no influence on mortality.

VIE-marked fish could not be individually identified through the course of the experiment, thus all data analyses for growth were conducted on tank mean values for species. The specific growth rate (SGR_w) by mass ($\%d^{-1}$) was calculated according to:

$$SGR_{wt} = 100(\ln W_2 - \ln W_1) / t, \quad (3.1)$$

where Wt_1 and Wt_2 are the mass in grams at the start and the end of the study period and t is the study period in days. The mass of all tagged fish was corrected for the PIT tag weight (by subtracting 0.1g for 12mm PIT tags and 0.6g for 23mm PIT tags). The specific growth rate for length (SGR_L) was calculated using the same formula as used for calculating mass.

Analysis of variance showed that initial fish length between treatments was significantly different for small chub ($F_{4,396} = 16.86$, $P < 0.001$), dace ($F_{4,395} = 11.14$, $P < 0.001$), roach ($F_{4,400} = 11.77$, $P < 0.001$) and large chub ($F_{2,298} = 3.56$, $P = 0.03$). As a result, SGR values were standardised against means of the previous sampling occasion to allow comparison using one-way ANOVA (*post hoc* test = LSD test or Dunnett T3 test if a Levene test revealed significantly unequal variance). All statistical analysis was carried out using SPSS (version 14.0) with a significance level $\alpha = 0.05$. Growth comparisons for large chub and small chub VIE treatments were not made because the initial size and tank density were not controlled.

6.3 Results

In total, 1606 hatchery-reared chub, dace and roach were subjected to nine different mark treatments for six months. Large variations in retention, survival and growth rate were observed at various stages of the experiment, influenced by mark type, fish size and mark location.

6.3.1 Mark retention

Considerable differences in retention rates were found between marks. PIT tag retention was highest over the six months of the experiment, with 100% retention for 12mm PIT tags in all three species and for 23mm PIT tags in both small and large chub. Two dace and one roach expelled the 23mm PIT tags, resulting in 96.6% and 98.7% retention, respectively. Throughout the experiment all PIT tags remained operational.

Mark location influenced VIE retention (Figure 6.1). Short-term (1 month) VIE retention was significantly better in the head than the fins of both dace (97.5% compared with 78.8%; χ^2 with continuity correction = 12.857, d.f. = 1, $P < 0.001$) and small chub (98.8% compared with 85.0%; χ^2 with continuity correction = 8.373, d.f. = 1, $P = 0.004$),

but not roach (96.3 % compared with 87.5 %; χ^2 with continuity correction = 3.014, d.f. = 1, $P = 0.083$). After six months, VIE mark retention in the head fell markedly (small chub 57.5%, dace 21.5%, roach 42.9%, large chub 29.6%) and was significantly higher in the fins (small chub 87.5%, dace 77.2%, roach 80.8%, large chub 88.8%) (χ^2 with continuity correction: small chub = 16.583, d.f. = 1, $P < 0.001$; large chub = 68.621, d.f. = 1, $P < 0.001$; dace = 46.225, d.f. = 1, $P < 0.001$; roach = 21.541, d.f. = 1, $P < 0.001$).

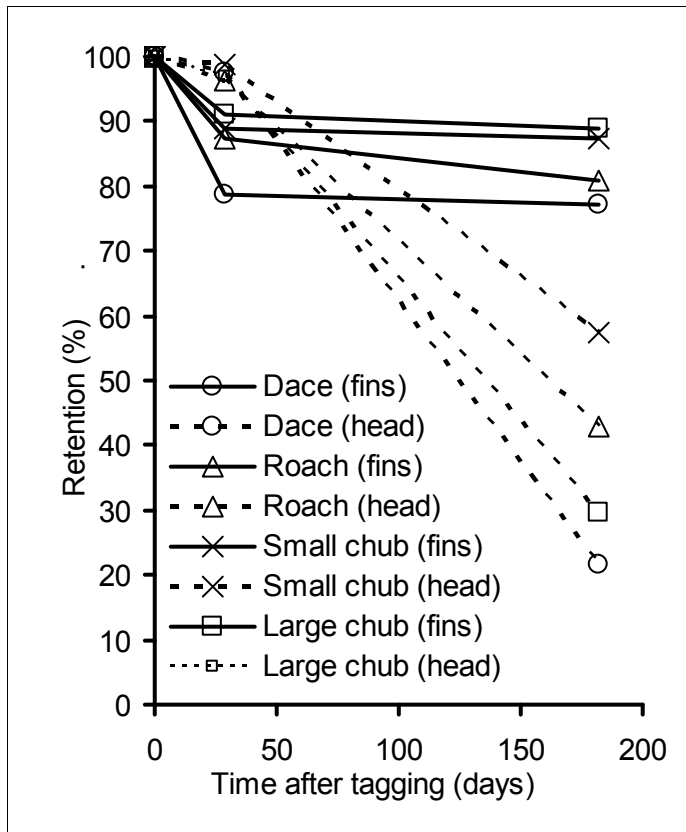


Figure 6.1 VIE retention (%) in head and fins of chub, roach and dace with time (days)

6.3.2 Survival

Only two roach (survival = 97.5%), two dace (97.5%) and one large chub (99%) marked with VIE died over the course of the experiment (Table 6.2). Survival was also high for small chub tagged with 23mm PITs – 96.3% survival compared with 100% for the control fish (Table 6.2). Two large chub tagged with 23mm PITs (no closure) died after 12 days and 127 days respectively (Table 6.3). Chub survival was not significantly different between marked and control groups ($\chi^2 = 5.229$, d.f. = 4, $P = 0.265$). Similar trends were observed for roach ($\chi^2 = 4.998$, d.f. = 4, $P = 0.287$; Table 6.4).

Survival of dace tagged with 23mm PITs and 12mm PIT sham-tagged dace was poor compared with small chub and roach (Table 6.5). Survival was significantly lower than controls on all sampling occasions because of high early mortality for 23mm PIT (Mann Whitney U -test: month 1: $Z = -3.365$, $n = 160$, $P < 0.001$; month 3: $Z = -3.090$, $n = 160$, $P = 0.002$; month 6: $Z = -3.319$, $n = 160$, $P = 0.001$) and 12mm PIT tag sham treatments (Mann Whitney U -test: month 1: $Z = -2.974$, $n = 160$, $P = 0.003$; month 3: $Z = -1.995$, $n = 160$, $P = 0.046$; month 6: $Z = -2.288$, $n = 160$, $P = 0.022$). This was not the case with VIE-marked and 12mm PIT-tagged dace. Mass at tagging influenced survival of 23mm PIT tagged dace ($t = -2.170$, $P = 0.033$) (Figure 6.2).

Table 6.2 Survival (% (*n*, no. of fish)), length (mean \pm SD, mm), mass (mean \pm SD, g), SGR and mark site condition for small chub treatments and control at 29 days, 89 days and 182 days post marking

Treatment	Control	VIE	12mm sham	12mm PIT	23mm PIT
Survival (%. (<i>n</i> , no. of fish)), after <i>n</i> days					
Initial <i>n</i>	80	80	81	80	80
29 d	100 (80)	100 (80)	98.8 (80)	100 (80)	100 (80)
89 d	100 (80)	100 (80)	98.8 (80)	100 (80)	97.5 (78)
182 d	100 (80)	100 (80)	97.5 (79)	97.5 (78)	96.3 (77)
Length (mean \pm SD, mm), after <i>n</i> days					
0 d	122.2 \pm 12.4	120.8 \pm 9.5	117.7 \pm 10.7	113.2 \pm 6.4	124.7 \pm 7.6
29 d	128.9 \pm 12.0	126.7 \pm 9.9	122.2 \pm 10.0	118.4 \pm 6.6	128.9 \pm 8.1
89 d	143.6 \pm 12.4	145.6 \pm 10.1	146.4 \pm 10.3	136.6 \pm 7.2	139.4 \pm 8.3
182 d	164.6 \pm 12.1	173.2 \pm 12.2	171.5 \pm 11.3	163.7 \pm 8.4	159.6 \pm 8.2
Mean SGR (% Ln day ⁻¹)					
dd 0-29	0.184	0.164	0.128	0.153	0.113
dd 29-89	0.181	0.231	0.301	0.238	0.131
dd 89-182	0.147	0.187	0.170	0.195	0.145
dd 0-182	0.164	0.198	0.207	0.203	0.135***
Mass (mean \pm SD, g), after <i>n</i> days					
0 d	22.8 \pm 7.7	20.9 \pm 5.5	19.1 \pm 4.9	16.8 \pm 3.0	22.9 \pm 4.9
29 d	26.3 \pm 8.4	23.9 \pm 6.2	19.1 \pm 5.2	19.2 \pm 3.4	27.3 \pm 17.5
89 d	39.4 \pm 10.3	41.8 \pm 9.0	45.1 \pm 10.1	32.1 \pm 5.3	32.6 \pm 6.1
182 d	58.0 \pm 13.4	69.0 \pm 15.2	65.3 \pm 14.1	54.9 \pm 9.3	52.4 \pm 8.7
Mean SGR (% Wt day ⁻¹)					
dd 0-29	0.486	0.466	0.005*	0.459	0.602
dd 29-89	0.677	0.935	1.432	0.851	0.297***
dd 89-182	0.415	0.537	0.399	0.578	0.509
dd 0-182	0.513	0.657	0.677	0.649	0.454*
Mean mark site condition, after <i>n</i> days					
29 d	-	0.00	0.14	0.06	0.48
89 d	-	0.00	0.00	0.00	0.00
182 d	-	0.00	0.00	0.00	0.00

Note: * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$ significantly lower than control.

Table 6.3 Survival (% (*n*, no. of fish)), length (mean \pm SD, mm), mass (mean \pm SD, g), SGR and mark site condition for large chub treatments and control at 29 days, 89 days and 182 days post marking

Treatment	Control	VIE (head + fin)	23mm PIT, no closure	23mm PIT, closure
Survival (%. (<i>n</i> , no. of fish)), after <i>n</i> days				
Initial <i>n</i>	100	99	101	100
29 d	100.0 (100)	100 (99)	99.0 (100)	100.0 (100)
89 d	100.0 (100)	99 (98)	99.0 (100)	100.0 (100)
182 d	100.0 (100)	99 (98)	98.0 (99)	100.0 (100)
Length (mean \pm SD, mm), after <i>n</i> days				
0 d	164.9 \pm 14.7	140.4 \pm 6.8	167.3 \pm 9.5	169.4 \pm 10.9
29 d	171.3 \pm 14.0	146.3 \pm 7.2	171.1 \pm 9.5	173.6 \pm 10.8
89 d	180.3 \pm 14.2	165.9 \pm 8.8	178.8 \pm 10.1	175.3 \pm 10.9
182 d	195.8 \pm 13.4	190.1 \pm 9.8	190.4 \pm 10.4	185.9 \pm 10.8
Mean SGR (% Ln day ⁻¹)				
dd 0-29	0.131	0.141	0.077	0.084
dd 29-89	0.084	0.209	0.073	0.016*** †††
dd 89-182	0.089	0.147	0.068*	0.063**
dd 0-182	0.094	0.166	0.071***	0.051*** †††
Mass (mean \pm SD, g), after <i>n</i> days				
0 d	56.6 \pm 15.1	35.3 \pm 5.4	58.0 \pm 10.1	60.7 \pm 12.5
29 d	56.5 \pm 14.3	34.0 \pm 5.4	61.6 \pm 11.0	66.6 \pm 13.5
89 d	82.3 \pm 18.7	68.9 \pm 11.1	73.1 \pm 14.3	63.8 \pm 13.1
182 d	101.9 \pm 21.2	96.6 \pm 15.0	89.5 \pm 15.9	82.2 \pm 15.8
Mean SGR (% Wt day ⁻¹)				
dd 0-29	-0.004	-0.035	0.197	0.318
dd 29-89	0.626	1.131	0.285***	-0.071*** †††
dd 89-182	0.230	0.363	0.219	0.272
dd 0-182	0.323	0.553	0.237***	0.166*** †††
Mean mark site condition, after <i>n</i> days				
29 d	-	0.00	0.59	0.61
89 d	-	0.00	0	0
182 d	-	0.00	0	0.01

Note: * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$ significantly lower than control; † = $P < 0.05$, †† = $P < 0.01$, ††† = $P < 0.001$ closure significantly lower than no closure.

Table 6.4 Survival (% (*n*, no. of fish)), length (mean \pm SD, mm), mass (mean \pm SD, g), SGR and mark site condition for roach treatments and control at 29 days, 89 days and 182 days post marking

Treatment	Control	VIE	12-mm sham	12mm PIT	23mm PIT
Survival (%. (<i>n</i> , no. of fish)), after <i>n</i> days					
Initial <i>n</i>	80	80	85	80	80
29 d	100.0 (80)	100.0 (80)	97.6 (83)	100.0 (80)	98.8 (79)
89 d	100.0 (80)	100.0 (80)	97.6 (83)	100.0 (80)	98.8 (79)
182 d	100.0 (80)	97.5 (78)	96.5 (82)	100.0 (80)	97.5 (78)
Length (mean \pm SD, mm), after <i>n</i> days					
0 d	118.1 \pm 6.3	120.4 \pm 7.1	117.7 \pm 6.4	116.3 \pm 5.3	122.6 \pm 6.8
29 d	120.1 \pm 6.3	122.6 \pm 7.2	120.5 \pm 6.5	118.9 \pm 5.4	124.9 \pm 7.2
89 d	128.4 \pm 6.8	129.9 \pm 7.5	131.6 \pm 7.4	127.5 \pm 5.8	128.0 \pm 7.6
182 d	135.4 \pm 6.7	141.3 \pm 8.3	141.0 \pm 8.6	138.1 \pm 6.5	134.2 \pm 8.3
Mean SGR (% Ln day ⁻¹)					
dd 0-29	0.058	0.063	0.079	0.077	0.065
dd 29-89	0.111	0.096	0.147	0.117	0.041***
dd 89-182	0.057	0.091	0.074	0.086	0.051
dd 0-182	0.075	0.088	0.099	0.095	0.050***
Mass (mean \pm SD, g), after <i>n</i> days					
0 d	22.8 \pm 4.2	24.1 \pm 5.3	21.9 \pm 4.2	21.2 \pm 3.4	24.7 \pm 5.5
29 d	23.1 \pm 4.0	24.6 \pm 5.2	20.6 \pm 4.1	22.4 \pm 3.4	25.3 \pm 5.3
89 d	32.3 \pm 4.9	34.9 \pm 7.4	37.2 \pm 7.2	32.0 \pm 4.6	28.7 \pm 5.3
182 d	38.0 \pm 7.7	42.7 \pm 9.2	41.3 \pm 8.7	38.4 \pm 6.1	35.0 \pm 7.2
Mean SGR (% Wt day ⁻¹)					
dd 0-29	0.043	0.072	-0.214*	0.196	0.086
dd 29-89	0.561	0.580	0.988	0.592	0.207***
dd 89-182	0.174	0.217	0.112	0.198	0.215
dd 0-182	0.281	0.313	0.349	0.328	0.192***
Mean mark site condition, after <i>n</i> days					
29 d	-	0	0.78	0.58	1.01
89 d	-	0	0.00	0.00	0.08
182 d	-	0	0.00	0.00	0.00

Note: * = $P < 0.05$, ** = $P < 0.01$, *** $P < 0.001$ significantly lower than control.

Table 6.5 Survival (% (*n*, no. of fish)), length (mean \pm SD, mm), mass (mean \pm SD, g), SGR and mark site condition for dace treatments and control at 29 days, 89 days and 182 days post marking

Treatment	Control	VIE	12-mm sham	12mm PIT	23mm PIT
Survival (%. (<i>n</i> , no. of fish)), after <i>n</i> days					
Initial <i>n</i>	80	81	80	80	80
29 d	97.5 (78)	98.8 (80)	83.8 (67) ††	100 (80)	78.8 (63) †††
89 d	93.8 (75)	98.8 (80)	83.8 (67) †	97.5 (78)	76.3 (61) ††
182 d	92.5 (74)	97.5 (79)	80.0 (64) †	96.3 (77)	72.5 (58) ††
Length (mean \pm SD, mm), after <i>n</i> days					
0 d	116.5 \pm 6.3	116.6 \pm 6.9	115.7 \pm 6.0	114.7 \pm 3.7	120.5 \pm 7.4
29 d	117.5 \pm 6.4	118.4 \pm 6.9	117.5 \pm 6.5	117.4 \pm 3.6	122.6 \pm 5.9
89 d	125.3 \pm 6.1	125.2 \pm 7.9	127.7 \pm 7.2	124.1 \pm 4.2	124.1 \pm 6.2
182 d	132.5 \pm 5.7	138.7 \pm 8.4	139.2 \pm 7.6	136.7 \pm 5.3	131.7 \pm 6.3
Mean specific growth rate (% Ln day ⁻¹)					
dd 0-29	0.030	0.052	0.053	0.079	0.059
dd 29-89	0.107	0.093	0.140	0.093	0.021***
dd 89-182	0.060	0.110	0.092	0.104	0.064
dd 0-182	0.071	0.095	0.102	0.096	0.049***
Mass (mean \pm SD, g), after <i>n</i> days					
0 d	16.4 \pm 3.1	16.0 \pm 3.7	15.6 \pm 3.0	15.3 \pm 1.8	17.5 \pm 4.7
29 d	16.3 \pm 3.2	16.8 \pm 4.6	13.9 \pm 3.0	17.7 \pm 16.2	18.0 \pm 3.4
89 d	23.0 \pm 3.6	25.2 \pm 5.8	28.6 \pm 5.5	23.1 \pm 3.7	20.2 \pm 3.7
182 d	28.9 \pm 4.3	34.0 \pm 6.5	33.9 \pm 5.3	31.5 \pm 4.1	27.6 \pm 4.9
Mean specific growth rate (% Wt day ⁻¹)					
dd 0-29	-0.003	0.162	-0.400	0.495	0.094
dd 29-89	0.570	0.678	1.203	0.446*	0.193***
dd 89-182	0.247	0.320	0.185	0.333	0.334
dd 0-182	0.313	0.413	0.428	0.396	0.249*
Mean mark site condition, after <i>n</i> days					
29 d	-	0.00	0.90	0.59	0.98
89 d	-	0.01	0.03	0.00	0.11
182 d	-	0.00	0.00	0.00	0.00

Note: † = $P < 0.05$, †† = $P < 0.01$, ††† = $P < 0.001$ Mann Whitney *U*-test, significantly lower than control.
* = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$ significantly lower than control.

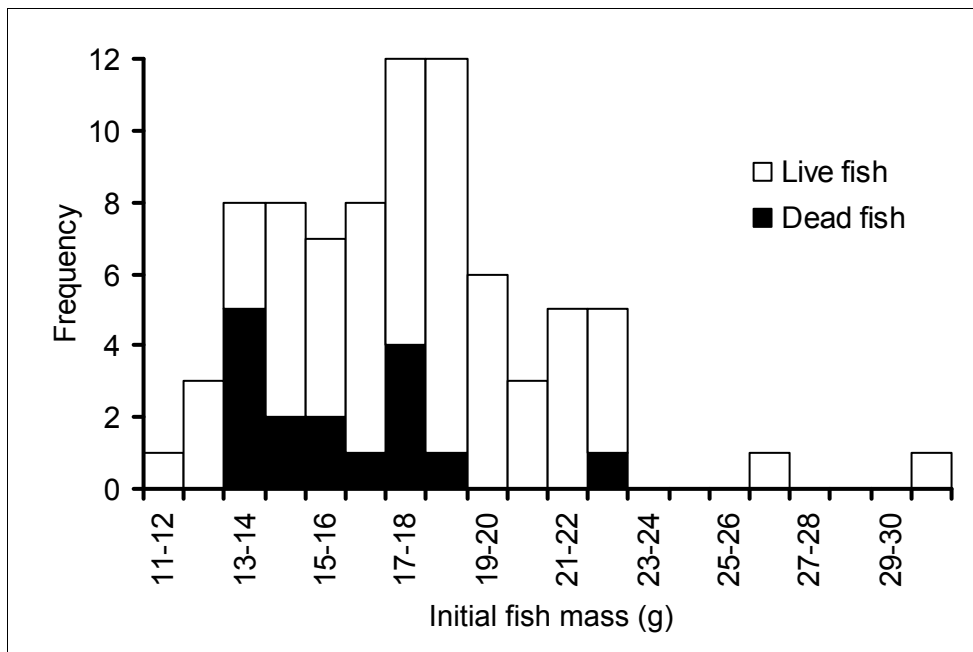


Figure 6.2 Mass frequency of initial size (g) at tagging for 23mm PIT-tagged dace, highlighting fish that died

6.3.3 Growth rate

Although restrictions on space and tanks prevented treatment replication, patterns of growth were similar in all trials: growth rates of both control and marked fish were generally lowest in the first month following marking, possibly indicating a handling effect (Tables 6.2-6.5).

Over the six-month period of the experiment, significant differences were found in SGRs among treatments for both length (ANOVA – small chub: $F_{4,390} = 57.522$, $P < 0.001$; dace: $F_{4,347} = 40.591$, $P < 0.001$; roach: $F_{4,399} = 31.639$, $P < 0.001$ and large chub: $F_{2,298} = 41.801$, $P < 0.001$) and mass (ANOVA – small chub: $F_{4,390} = 53.116$, $P < 0.001$; dace: $F_{4,347} = 38.316$, $P < 0.001$; roach: $F_{4,399} = 20.282$, $P < 0.001$ and large chub: $F_{2,298} = 50.874$, $P < 0.001$). The main period of reduced growth for 23mm PIT tagged fish compared with controls was in months 1–3 (Figure 6.3). However, similar SGRs between control and treatments for months 3–6 suggest that the long-term growth effects on 23mm PIT-tagged fish were small.

6.3.4 Mark site condition

The VIE mark site condition was nearly always excellent (Table 6.3). Incision trauma scores remained elevated for longer for 23mm PIT tag sites than for 12mm PIT tag sites, indicating that the larger incision was associated with greater inflammation and took longer to heal completely (Tables 6.2, 6.4 and 6.5). Applying adhesive closure to 23mm PIT-tagged large chub had no influence on the rate of wound healing or chronic wound inflammation (Table 6.3).

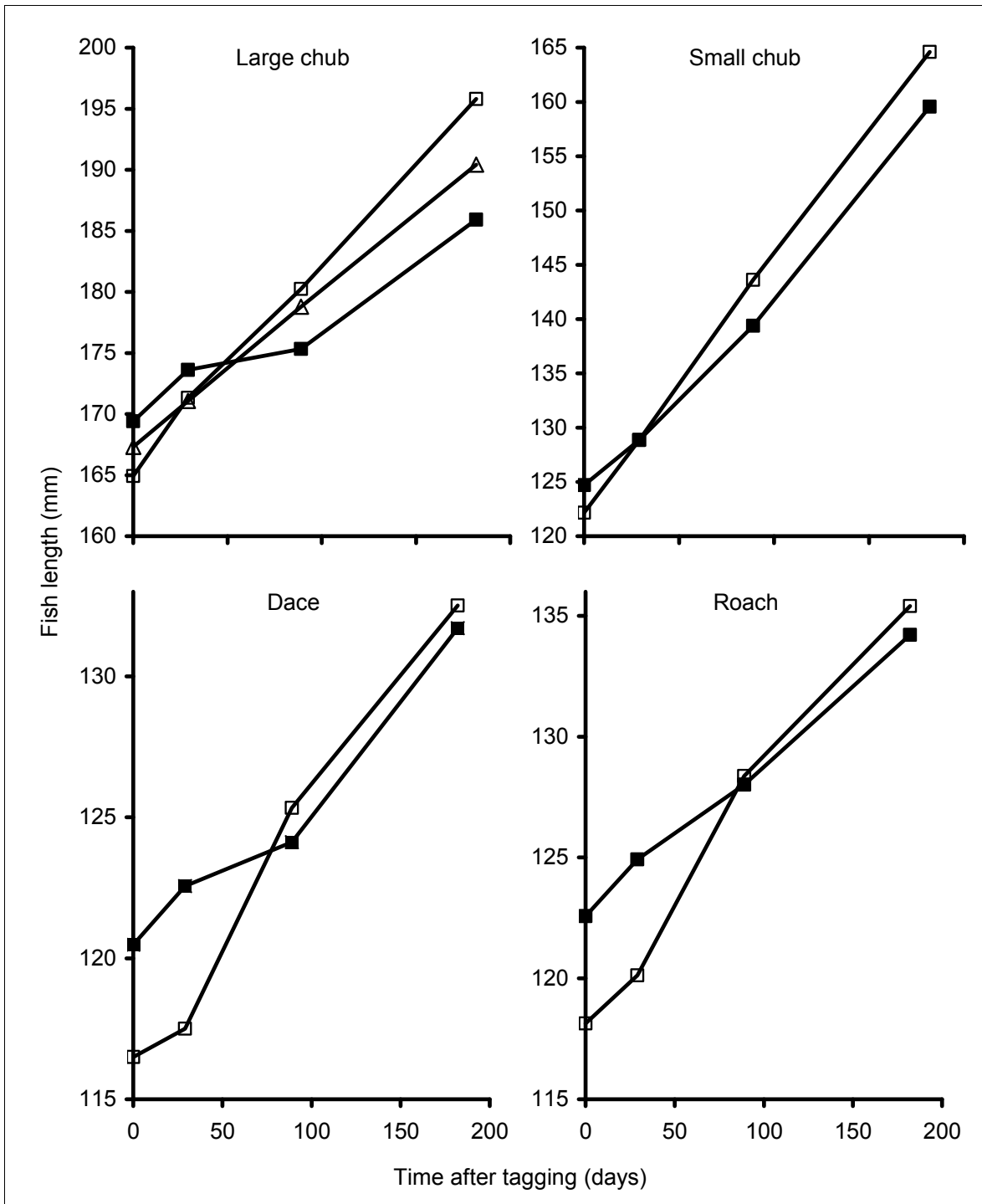


Figure 6.3 Mean length (mm) of chub, dace and roach at time (days) after tagging for control (□), 23mm PIT with adhesive closure (■) and 23mm PIT without closure (△)

6.4 Discussion

Mark retention in chub, roach and dace varied markedly in relation to mark type, body location, and fish species and size. The relationship between mark type and application and the fish species and size also had a substantial effect on the survival and growth of these cyprinids. The 12mm PIT tagging had several benefits over VIE for marking juvenile cyprinids, including high tag retention and functionality, negligible tagging mortality and no apparent long-term effects on growth. Growth retardation, mostly during the first three months after tagging, was recorded for fish implanted with 23mm PIT tags, with small dace suffering elevated mortality with these larger PIT tags.

6.4.1 Effects of mark type, location and size of fish on retention

VIE mark retention was higher in the head than in the fins over the short term (one month) but declined thereafter, whereas retention in the fins was constant over the long term. Similar findings were reported by Dewey and Zigler (1996) and Brennan *et al.* (2005). By contrast, Bonneau *et al.* (1995) and Farooqi and Morgan (1996) found high levels of retention in both the head and fins of bull trout (*Salvelinus confluentus* (Suckley)) (4 months) and barbel (2 months). Increasing loss of the VIE marks over time after good initial retention has also been found for other marking locations (Bailey *et al.* 1998; Close and Jones 2002; Fitzgerald *et al.* 2004; Goldsmith *et al.* 2003; Hale and Gray 1998).

The long term retention rates in fins (>80%) compare favourably with other studies: 97% in brown trout (Summers *et al.* 2006), 96% in rainbow trout (*Oncorhynchus mykiss* (Walbaum); Walsh and Winkelman 2004) and 70% in adult black bream (*Acanthopagrus butcheri* (Munro); Doupe *et al.* 2003). Applying VIE to the fins of smaller cyprinids was more difficult than applying it under the dermal tissue overlying the cranium, because of the thinness of the tissue. However, long-term retention was much better with the former and shows the importance of adopting an adequate experimental trial period.

Variable VIE retention for different implantation sites has been attributed to: the inexperience of the people marking the fish; damage to the marking site during injection; handling related losses; loss or fragmentation during fish growth and swimming activity; the elastomer not solidifying; and/or the implantation wound not healing quickly (Farooqi and Morgan 1996; Frederick 1997; Hale and Gray 1998; Willis and Babcock 1998; Bailey *et al.* 1998; Astorga *et al.* 2005; Thompson *et al.* 2005). Elastomer loss from the head may increase with time because it can be forced out as the fish grow (Goldsmith *et al.* 2003). The differing VIE retention in fin and head tissues in this study may relate to the degree of porosity in the target tissue, causing migration of the elastomer (Brennan *et al.* 2005).

In this study, VIE retention was similar for both large and small chub. In contrast, other research groups have suggested that elastomer loss occurs more often in small fish because the target site is too fragile or the smaller target site requires more precise application (Bailey *et al.* 1998; Hale and Gray 1998; Olsen and Vollestad 2001; Close 2000). To reduce the impact of initial losses on field experiments, an 18-day laboratory wound healing/elastomer hardening period has been recommended (Thompson *et al.* 2005; Brennan *et al.* 2005). In addition, less than 100% retention is acceptable if the detection rate over time is known. Therefore, a sub-sample of fish could be monitored in a laboratory environment during a field study (Close 2000), since Brennan *et al.* (2005) reported no differences in VIE retention between field and laboratory trials.

Tags surgically implanted into the peritoneal cavity can be expelled through the body wall (Lucas 1989; Moore *et al.* 1990) via transintestinal expulsion (Summerfelt and

Mosier 1984; Chisholm and Hubert 1985; Marty and Summerfelt 1986; Baras and Westerloppe 1999) or during spawning in females (Prentice *et al.* 1990a). In this study, 100% retention rates of 12mm tags were observed, similar to rates reported for Atlantic salmon parr (Juanes *et al.* 2000; Gries and Letcher 2002; Riley *et al.* 2003) and bullhead (*Cottus gobio* (L.)) (Bruyndoncx *et al.* 2002).

Retention of 23mm PIT tags was also high (>96.6%) in this study and was not significantly affected by fish size and species or wound closure. These results are comparable with those of Zydlewski *et al.* (2001) for surgically implanted 23mm PIT tags in salmon parr >9cm (99%). Roussel *et al.* (2000) reported high retention of 23mm PITs in Atlantic salmon parr >8.4cm, but found that sutures increased tag retention in fish with lengths of 6.4–8.4cm. Gries and Letcher (2002) reported the need to make the incision small enough so that the tag cannot easily work its way out. Buzby and Deegan (1999) found instantaneous tag losses were often linked to poor tag placement and suggested that PIT tags may be retained for the life of the fish if they are not rejected soon after implantation.

6.4.2 Effects of marking on survival

The survival of all marked cyprinids in the present study was high and similar to the unmarked control fish, except for the 23mm PIT-tagged dace. This finding is consistent with previous studies that observed negligible mortality when using VIE marks on fish (Farooqi and Morgan 1996; Dewey and Zigler 1996; Olsen and Vollestad 2001; Bruyndoncx *et al.* 2002; Astorga *et al.* 2005). Similarly high survival rates were found up to nine months after tagging following surgical implantation of 12mm and 23mm PIT tags into the peritoneal cavity of salmonids (Zydlewski *et al.* 2001; Gries and Letcher 2002; Riley *et al.* 2003), Nile tilapia (*Oreochromis niloticus* (L.)) (Baras *et al.* 1999), juvenile perch (Baras *et al.* 2000) and bullhead (Bruyndoncx *et al.* 2002).

The high dace mortality rate observed in this study appears to be related to the fish mass at tagging, with smaller fish more prone to dying. However, the condition of the dace at the start of the experiment was poor, with fin erosion and scale loss seen on a number of individuals. Higher mortalities were also found in smaller sized Atlantic salmon parr surgically implanted with 23mm PITs (Roussel *et al.* 2000).

With the exception of dace, the mortality rates of marked fish are unlikely to have an impact on experimental studies relying on recaptures, by lowering the probability of recapture and potentially leading to over-estimates of population size when using mark-recapture calculations (Woods and Martin-Smith 2004). The initial small mortality was probably the result of stress from either handling and/or anaesthesia (Ombredane *et al.* 1998; Brennan *et al.* 2005; Willis and Babcock 1998; Gries and Letcher 2002; Dussault and Rodriguez 1997), whilst any later mortality was more likely caused by other factors, such as the holding facilities, fish density (Malone *et al.* 1999) and length of study (Gries and Letcher 2002).

6.4.3 Effects of marking on fish growth

Growth is a more sensitive indicator than mortality of chronic physiological stress or trauma caused by marking (Malone *et al.* 1999). Growth is an important consideration when selecting the type of mark to use, particularly in animals that are to be released into the wild to serve as indicators of various biological parameters in the natural population (Woods and James 2003). Any reduced fitness in the study animal may lessen the validity of the collected data (Cote *et al.* 1999). However, detecting marginal growth depression in marked fish is often difficult because of high levels of variation between individuals and/or experimental units (Woods and Martin-Smith 2004).

No significant effect on growth of VIE marking or implanting 12mm PITs was found during this study. Similarly, no growth depression was found in other studies using fish marked with elastomers (Bailey *et al.* 1998; Olsen and Vollestad 2001; Dewey and Zigler 1996; Thompson *et al.* 2005; Astorga *et al.* 2005) or 12mm PITs (Peterson *et al.* 1994; Ombredane *et al.* 1998; Juanes *et al.* 2000; Das Mahapatra *et al.* 2001).

It was hypothesised that the greatest effects of marking on growth would be for 23mm PIT-tagged small cyprinids, because of the large incision relative to body size (Baras *et al.* 2000) and the larger tag relative to fish size. It is generally accepted that the internal transmitter weight should not exceed 2% of the fish body mass (Winter 1996; Swanberg and Geist 1997; Walsh *et al.* 2000), although there is increasing recognition that smaller fishes can often cope with a higher loading without ill effect (Claireaux and Lefrançois 1998; Martinelli *et al.* 1998; Brown *et al.* 1999; Cote *et al.* 1999; Jepsen *et al.* 2001, 2002). In this study, the tag weight exceeded 2% body mass for all of the small 23mm PIT-tagged fish (Table 6.1), with the highest tag-to-body-mass ratios in dace. Although restrictions on space and tanks prevented treatment replication for groups of the same-sized fish, small but significant reductions in growth rate were recorded for all groups of cyprinids tagged with 23mm PIT tags (three tanks) over the six-month period.

Typically, the growth of 23mm PIT-tagged cyprinids was suppressed during the first three months after tagging, but they then experienced similar growth to controls in the period 3–6 months after tagging. This change in response may have occurred because the physiological stress response to surgery reduces with time (Jepsen *et al.* 2001) and because growth reduces the tag/body mass ratio (Adams *et al.* 1998) and the detrimental effects on buoyancy (Perry *et al.* 2001). Additionally, larger fish can accommodate the tag better, reducing pressure in the stomach and allowing unimpeded food consumption (Lacroix *et al.* 2004).

In the large chub treatments, fish without adhesive closure of the incision grew significantly faster than those with adhesive closure. Although chub with adhesive closure experienced lower growth over the six months, their growth was markedly higher in the first month after tagging and longer term effects would not be expected to be directly attributable to the adhesive. Skov *et al.* (2005) noted no impact of 23mm PIT tags applied without tissue adhesive on the survival and growth of roach and rudd and there may be little or no benefit of tissue adhesive for this purpose.

6.5 Conclusions and field study recommendations

In summary, PIT tags are effective and reliable. They provide the the most suitable method for marking individual juvenile chub, dace and roach at modest cost, potentially providing high spatial and temporal resolution of data. VIE implantation in fins could provide a cheap, batch-marking alternative, as long as retention rates are monitored.

The size distribution of fish marked in this experiment covered the range of sizes typically stocked into river fisheries, thereby ensuring that the results are applicable to marking studies on stocked fish. Small cyprinids (>9cm fork length) can be tagged with 12mm PIT tags and slightly larger fish (>12cm fork length) with 23mm tags, with minimal concerns over retention, mortality or long-term growth. However, hatchery fish are not exposed to the same stresses as encountered in a natural environment (predation, density and feeding), thus survival and growth may be artificially elevated in a controlled setting (Gries and Letcher 2002).

This possibility is perhaps most relevant for dace, which is the most sensitive to capture and handling out of the three species studied, experiencing higher incidences of scale loss and fin damage. Although the use of 12mm PIT tags would be preferred for mark-recapture purposes given their negligible recorded effects on fish health, the range advantages of 23mm PIT tags for telemetry applications (Lucas and Baras 2000; Zydlewski *et al.* 2001) probably outweigh any minor effects on growth.

7 Dispersal of stocked cyprinids in a small English river: comparison to wild fish using a multi-method approach

7.1 Introduction

Movement of animals, a process which is rarely random (Kramer *et al.* 1997), affects individual fitness via growth and survival, but it also influences the distribution and abundance of a population, with genetic and evolutionary consequences. Thus, with respect to fish in stream and river environments, a sound understanding of their movements and the factors affecting this movement is crucial for managing and conserving populations, especially in relation to habitat fragmentation (Lucas and Baras 2001).

Historically, field studies have used mark-recapture to document the pattern of distribution and extent of movement of stream fishes. These studies have tended to conclude that populations are composed of both sedentary and highly mobile individuals (Gerking 1953; Gowan *et al.* 1994; Rodriguez 2002). However, although mark-recapture studies offer value in monitoring movement and survival, they are biased by the location and timing of the recapture efforts, potentially leading to erroneous conclusions (Lucas and Baras 2000). Recently, greater attention has been paid to the mechanisms that trigger movement in stream fishes. However, the influence of environmental variation (flow and temperature) remains poorly understood, especially during non-breeding periods (but see Albanese *et al.* 2004).

Stocking with hatchery-reared fish is one of the primary actions taken in response to poor fishery performance. It can be undertaken to compensate for loss of stock due to fish mortality or environmental degradation, or as part of a rehabilitation programme (Cowx 1994). Post-stocking evaluations have mainly involved salmonids and indicated limited benefits of stocking (Huntingford 2004). For example, studies have suggested that stocked fish may disperse rapidly from their initial stocking location (Arctic grayling, *Thymallus arcticus* (Pallas); Thorfve 2002), particularly during high flow events (rainbow trout; Bettinger and Bettoli 2002). It has also been suggested that the persistence of cyprinids stocked into rivers is low (Axford 1974; Barnard *et al.* 2002; Aprahamian *et al.* 2004).

However, the methods used in previous Environment Agency studies to assess the fate of cyprinids stocked into rivers have suffered the potential biases identified above. This has been compounded by difficulties in recapturing sufficient fish and in reliably identifying individuals. For example, the study of Aprahamian *et al.* (2004) recorded low persistence of stocked cyprinids. However, the extent of sampling was such that if the fish were strongly aggregated, as is typical of juvenile cyprinids, it would be easy to record low recapture rates by chance alone, falsely implying a low level of persistence. Such an effect is much less likely with more widely-spaced, territorial, stream-dwelling salmonids.

The behaviour of stocked cyprinids compared to wild fish has not been widely investigated. Behavioural deficits and naivety in avoiding predation have been identified in hatchery-reared salmonids (Huntingford 2004), but knowledge and understanding of spatial behaviour and the influence of environmental variables is lacking, especially for stocked non-salmonid river fishes. Of particular interest is the response of stocked fish to elevated flows, since these fish may be less able to resist high flows than resident, wild fish (MacDonald *et al.* 1998; Cowx *et al.* 1986).

Rearing fish for stocking incurs substantial costs (Barnard *et al.* 2002) and significant ecological and/or fisheries benefits may not be achieved if the survival and persistence of stocked fishes is low. Ultimately, *in situ* comparisons of movement, site fidelity and survival between hatchery-reared fish and wild populations are crucial to improve the effectiveness of stock enhancement measures.

Although little is known regarding the movements of stocked cyprinids, several radio telemetry studies have examined space use by wild chub (for example, Fredrich *et al.* 2003), dace (for example, Clough and Ladle 1997; Clough and Beaumont 1998) and roach (Baade and Fredrich 1998). However, these studies were limited by small samples of large fish. Hence, information is needed to improve understanding of the spatial behaviour of wild juvenile cyprinids in lowland rivers during non-breeding periods.

This study used radio-telemetry to compare the short-term movements and habitat selection of stocked fish with those of wild juvenile chub, under both normal and elevated flows. In addition, PIT tags (Prentice *et al.* 1990a, b), which allow monitoring of individual fish and are suitable for tagging relatively large samples of small fish, were used for mark-recapture and fixed station telemetry (Zydlewski *et al.* 2001), in order to determine the space use and survival of wild and stocked cyprinids. It was hypothesised that stocked fish would move more than wild fish because the former are being released into an unfamiliar environment with no opportunity to develop spatial mapping of their surroundings, unlike wild fish.

Specifically, the objectives were to: 1) compare the movements of wild cyprinids between two consecutive winters; 2) compare the movements of wild and stocked chub and roach during the second winter; and 3) evaluate the timing and direction of fish movements and how they are influenced by temperature and flow (including flood scenarios). The results are discussed in terms of the proximate mechanisms influencing individual movement, under the assumption that animals make movement decisions at least in part to increase their fitness (Kramer *et al.* 1997).

7.2 Methods

7.2.1 Study site

The study was carried out on the River Roding in south-east England between October and March in both 2005–06 and 2006–07. The River Roding rises at an altitude of 110m above sea level (51°53'59"N 0°16'19"E) and flows south for approximately 80km to join the tidal River Thames at Barking Creek (51°24'47"N 0°16'19"E). It drains a predominately clay agricultural catchment (340km²). The study site was a 10km section of the river, approximately 20km from the source. This river section was mostly 5–8m wide with an alternating riffle/glide (20–40cm depth) and pool (<150cm depth) topography, although there are some wider and deeper areas.

Wheypules Mill (51°77'05"N 0°30'59"E), which is at the upstream end of the study section, acts as a barrier to upstream fish movement. Fyfield Mill (51°44'13"N

0°16'26"E), which is approximately 6km from the top of the study reach, also acts as a barrier to upstream fish movements. However, downstream movements are possible, especially under elevated flow when a sluice gate is opened manually. There is no obstruction to downstream movement for at least 10km, although a flat-v flow-gauging weir (51°42'47"N 0°15'29"E) is present 4km downstream of the second mill and represents the downstream limit of the study reach. Extensive areas of instream macrophytes and overhanging and submerged terrestrial vegetation are found all along the study reach.

The River Roding exhibits a typical flow regime for a small temperate lowland river, with low summer flows and highly variable winter flows. Flow rises rapidly in response to substantial rainfall in the catchment. Mean daily flow ($\text{m}^3 \text{s}^{-1}$) was measured at 15-minute intervals at the gauging weir and the water temperature was recorded at 15-minute intervals using a logger (Tinytalk, Orion Components, Chichester, UK). The mean daily flow in each of the two years (2005 = $0.129 \text{m}^3 \text{s}^{-1}$ and 2006 = $0.613 \text{m}^3 \text{s}^{-1}$) was used to calculate the magnitude of flow peaks observed during the study periods. During the 2006–07 study period, six periods of elevated flow (greater than 6.9 times normal flow) were observed, with the largest peak reaching ≈ 14.4 times normal flow (14 February 2007). No such events occurred in 2005–06.

In June 2003, a polluting incident in the River Roding, 12km upstream of the study site, resulted in an oxygen sag that killed several thousand fish up to 20km downstream. The pollution did not markedly affect invertebrate communities, which recovered within the same year (Environment Agency, unpublished data).

In December 2003, approximately 1000 hatchery-reared, unmarked chub (age 1+ and 2+), dace (1+) and roach (1+) were stocked in the river to aid recovery. Subsequent electric fishing surveys in summer and autumn 2005 found a wide range of species throughout the study reach, many of which had not been stocked, including bullhead, stone loach, minnow, eel (*Anguilla Anguilla* (L.)), gudgeon, perch, rudd, tench, and pike, as well as chub, dace and roach. Thus, a substantial proportion of the fish community in the study reach survived or recolonised the reach following the pollution event, potentially augmented by the stocked fish. Despite this, fish stocks in the area remained below recent historical levels (Environment Agency, unpublished data) and presumably below carrying capacity. It was therefore felt that additional stocking was required to aid further recovery of the fishery and to study the behaviour of stocked fish.

It should be noted that 'wild' fish were either progeny of adults that spawned in the River Roding or fish that had been stocked in December 2003. It was not possible to distinguish wild fish from those that had been stocked into the river and naturalised.

7.2.2 Sampling and tagging procedure

Wild fish were obtained from the study reach in both 2005 and 2006 using pulsed DC (50Hz) electric fishing equipment (Electracatch control box, 1.5V single anode with Honda 1kVA generator, or Electracatch control box, 6V twin anode with Honda 7.5kVA generator). The fish were caught from a boat or by wading into the river (Table 7.1). Representative sampling sites (approximately 200m long) were selected, comprising riffle, glide and pool habitats. Natural morphological limiters of fish escape (riffles or channel bottlenecks) were used to de-limit each section. Once selected, site locations were consistent throughout future sampling occasions. Wild chub for radio tracking ($n = 21$ in 2005 and $n = 15$ in 2006) were obtained from the 1km section of the study reach around the most downstream stocking location.

Table 7.1 Summary of electric fishing surveys for tagging wild fish, including the date sampled, number of sites fished, total length of river fished (m), mean site length (m ± SD) and the number of fish (all species) tagged

Sampling date	Number of sites	Total length of river sampled (m)	Mean site length (m ± SD)	Number tagged (all species)
19/10 – 1/11/2005	29	5890	203.1 ± 78.7	546
2/12 – 8/12/2005	19	3160	166.3 ± 49.0	210
11/03 – 17/03/2006	33	6330	191.8 ± 74.8	206
28/10 – 2/11/2006	19	3650	192.1 ± 74.8	328

Chub, roach and dace were tagged with 12mm or 23mm PIT tags. Small (12mm) PIT tags can be used to tag fish as small as 6cm (Lucas and Baras 2000) and are ideal for mark-recapture, while larger (23mm) PIT tags have a greater range and offer advantages for fixed-station telemetry of larger fish (Lucas and Baras 2000; Zydlewski *et al.* 2001). Previous studies of cyprinids (Skov *et al.* 2005; Chapter 6) have reported high long-term survival for fish larger than 12cm tagged with 23mm PIT tags.

By implanting PIT tags, the movements (including direction) of large numbers of individual fish were monitored continuously using fixed-location stations, while their survival and distribution after each winter were assessed using mark-recapture. In addition, radio transmitters were implanted in chub larger than 15cm to provide detailed information on short-term movement and habitat selection.

Prior to tagging in the field, fish were anaesthetised using buffered tricaine methane-sulphonate (MS-222, 0.1 g L⁻¹), and their body mass (g) and fork length (mm) were recorded (Tables 7.2–7.4). Fish were placed ventral side up in a clean V-shaped foam support with their gills submerged in fresh, oxygenated water. Tags were sterilised with alcohol and rinsed with distilled water prior to use. As described in Chapter 6, 12mm tags were inserted into the body cavity through a 3mm-long ventro-lateral incision made with a scalpel, 2–3 mm anterior to the muscle bed of the pelvic fins. The 23mm tags were inserted in to the body cavity in a similar way, through a 5mm-long ventro-lateral incision. Due to the small size of the incisions, they were not closed (Skov *et al.* 2005). Additionally, a small Panjet (Wright Dental Group, Dundee, UK) was used to apply an Alcian blue mark anterior to the pelvic fins, in order to provide an estimate of tag loss. PIT tag weight/body mass ratios are given in Tables 7.2–7.4. Fish were held in a well-aerated observation tank until they regained their balance and were observed actively swimming, after which they were returned to the river at the approximate site of capture.

Radio transmitters (type PIP, 19mm x 9mm x 6 mm with a 12cm long, 0.1mm diameter whip antenna, potted in medical grade silicone, 1.2g weight in air, expected life of 45 days; Biotrack, Wareham, UK) were inserted into chub. This involved placing the chub ventral side up in a surgical trough and irrigating their gills with a diluted dose of anaesthetic, until the final minute of the procedure when only fresh water was supplied. Prior to surgery, fork length (mm) and body mass (g) were recorded, and the unique frequency (between 173.200MHz and 173.970MHz, with a nominal spacing of 10kHz) of each transmitter was verified using a hand-operated receiver. An 8–10mm-long ventro-lateral incision was made anterior to the muscle bed of the pelvic fins and the whip antenna was run via the incision in the body cavity to the exterior, posterior to the pelvic fins, using a shielded needle. The transmitter was then inserted into the body cavity. A 23mm, half-duplex PIT tag was also inserted into the fish, providing verification of fish location by remote monitoring stations and, in some cases, evidence of radio-tag failure. The incision was closed with two or three separate absorbable sutures. The procedure lasted approximately six minutes in total.

Table 7.2 Number (n), length (mean \pm SD (range), mm), mass (mean \pm SD (range), g) and ratio (%) of tag weight of wild and stocked chub

Treatment / release date	n	Fish length (mean \pm SD (range), mm)	Fish mass (mean \pm SD (range), g)	Tag / body wt ratio (mean (range), %)
Wild 12mm PIT				
Oct-05	13	216.2 \pm 96.1 (112–373)	209.7 \pm 245.3 (14–633)	0.05 (0.02–0.71)
Dec-05	20	250.3 \pm 85.1 (132–470)	301.9 \pm 361.2 (25–1500)	0.03 (0.01–0.40)
Mar-06	23	212.5 \pm 56.7 (119–348)	163.9 \pm 157.2 (18–686)	0.06 (0.01–0.56)
Oct-06	11	234.1 \pm 119.1 (113–446)	236.1 \pm 306.9 (16–894)	0.04 (0.01–0.63)
Wild 23mm PIT				
Oct-05	81	256.7 \pm 75.3 (135–472)	323.0 \pm 320.9 (29–1474)	0.19 (0.04–2.07)
Dec-05	56	248.6 \pm 36.4 (168–383)	215.1 \pm 124.6 (54–872)	0.28 (0.07–1.11)
Mar-06	56	242.0 \pm 67.0 (139–490)	241.5 \pm 242.9 (39–1132)	0.28 (0.05–1.54)
Oct-06	36	253.5 \pm 73.7 (132–435)	287.3 \pm 273.2 (28–1274)	0.21 (0.05–2.14)
Wild radio tagged				
Oct-05	21	199.7 \pm 31.3 (153–243)	106.5 \pm 49.8 (44–198)	0.02 (0.01–0.04)
Oct-06	15	188.3 \pm 24.1 (158–239)	96.9 \pm 40.5 (48–172)	0.02 (0.01–0.04)
Stocked 23mm PIT				
Nov-06 S1	175	143.9 \pm 8.1 (109–171)	38.5 \pm 6.9 (16–66)	1.56 (0.91–3.87)
Nov-06 S2	175	143.3 \pm 8.1 (115–176)	38.3 \pm 6.9 (17–68)	1.57 (0.88–3.47)
Nov-06 S3	175	147.6 \pm 11.5 (128–183)	42.7 \pm 11.4 (27–80)	1.41 (0.75–2.24)
Stocked radio tagged				
Nov-06 S3	15	168.0 \pm 6.7 (158–178)	65.0 \pm 7.2 (54–77)	0.03 (0.02–0.03)
Stocked Alcian blue control				
Nov-06	225	144.7 \pm 8.9 (111–169)	38.7 \pm 7.6 (16–61)	-

Table 7.3 Number (n), length (mean \pm SD (range), mm), mass (mean \pm SD (range), g) and ratio (%) of PIT tag weight of wild and stocked dace

Treatment / release date	n	Fish length (mean \pm SD (range), mm)	Fish mass (mean \pm SD (range), g)	Tag / body wt ratio (mean (range), %)
Wild 12mm PIT				
Oct-05	28	124.3 \pm 16.3 (100–177)	22.5 \pm 15.8 (10–92)	0.44 (0.11–1.00)
Dec-05	10	142.5 \pm 24.8 (110–178)	38.0 \pm 19.1 (15–63)	0.26 (0.16–0.67)
Mar-06	19	142.2 \pm 28.2 (110–192)	40.4 \pm 29.2 (12–100)	0.25 (0.10–0.83)
Oct-06	10	178.5 \pm 33.7 (122–224)	84.4 \pm 48.1 (20–171)	0.12 (0.06–0.50)
Wild 23mm PIT				
Oct-05	118	256.7 \pm 75.3 (135–472)	323.0 \pm 320.9 (29–1474)	0.19 (0.04–2.07)
Dec-05	23	248.6 \pm 36.4 (168–383)	215.1 \pm 124.6 (54–872)	0.28 (0.07–1.11)
Mar-06	42	242.0 \pm 67.0 (139–490)	241.5 \pm 242.9 (39–1132)	0.28 (0.05–1.54)
Oct-06	72	253.5 \pm 73.7 (132–435)	287.3 \pm 273.2 (28–1274)	0.21 (0.05–2.14)

Table 7.4 Number (n), length (mean \pm SD (range), mm), mass (mean \pm SD (range), g) and ratio (%) of PIT tag weight of wild and stocked roach

Treatment / release date	n	Fish length (mean \pm SD (range), mm)	Fish mass (mean \pm SD (range), g)	Tag / body wt ratio (mean (range), %)
Wild 12mm PIT				
Oct-05	91	119.4 \pm 27.2 (87–233)	25.8 \pm 28.7 (11–216)	0.39 (0.05–0.91)
Dec-05	52	136.9 \pm 20.9 (93–180)	40.8 \pm 19.3 (13–93)	0.25 (0.11–0.77)
Mar-06	18	134.4 \pm 21.6 (107–198)	41.2 \pm 26.1 (16–135)	0.24 (0.07–0.63)
Oct-06	69	128.2 \pm 22.9 (103–220)	36.8 \pm 29.9 (12–214)	0.27 (0.05–0.83)
Wild 23mm PIT				
Oct-05	215	167.9 \pm 36.9 (113–307)	88.2 \pm 80.4 (20–547)	0.68 (0.11–3.00)
Dec-05	49	156.3 \pm 25.4 (117–245)	66.0 \pm 46.9 (22–272)	0.91 (0.22–2.73)
Mar-06	48	151.2 \pm 23.7 (113–209)	60.2 \pm 35.4 (21–166)	1.00 (0.36–2.86)
Oct-06	130	167.3 \pm 29.1 (117–239)	82.0 \pm 47.3 (22–234)	0.73 (0.26–2.73)
Stocked 23mm PIT				
Nov-06 S1	174	126.2 \pm 6.7 (106–153)	34.1 \pm 6.1 (20–76)	1.76 (0.79–3.00)
Nov-06 S2	174	126.8 \pm 6.8 (112–152)	35.0 \pm 6.1 (21–60)	1.71 (1.00–2.86)
Nov-06 S3	175	126.2 \pm 7.3 (108–165)	33.4 \pm 6.5 (19–71)	1.80 (0.85–3.16)
Stocked Alcian blue control				
Nov-06	225	125.4 \pm 6.9 (88–157)	32.8 \pm 6.2 (10–70)	-

All fish were treated in compliance with the UK Animals (Scientific Procedures) Act 1986; Home Office licence number PPL 60/3260.

Stocked fish were the progeny of broodstock taken from the River Bain in eastern England (chub) and a lake in north eastern England (roach). They were reared in the hatchery and pond facilities of the Environment Agency's Calverton Fish Farm in Nottingham.

Fish were exposed to flow in all rearing environments. The age (1+) and size distributions (Tables 7.2 and 7.4) of fish tagged in this experiment were representative of sizes usually stocked into UK rivers, ensuring that the results would be applicable to future fish stocking programmes. Stocked fish were tagged with 23mm PIT tags at the fish farm two weeks prior to release using the same procedure described above but were allowed to recover in indoor tanks (capacity 2.02 m³) supplied with filtered groundwater (60L⁻¹ min⁻¹ tank⁻¹). In addition, 225 fish of each species were not implanted with a PIT tag but were marked with Alcian blue dye posterior to the pelvic fins, to act as a tagging control (Tables 7.2 and 7.4).

Until the day prior to release, fish were fed approximately 3% of their body mass per day using automatic feeders, supplemented by natural frozen gamma-radiated feed. The fish were transported in large aerated containers and released into the river on 3 November 2006. Stocking locations (S1 to S3) were 1450m, 4150m and 7160m from the upstream limit of the study section. A total of 550 1+ hatchery-reared chub and 525 1+ hatchery-reared roach – PIT-tagged (23mm) and marked with Alcian blue dye – were stocked in equal numbers at the three locations along the study river (Tables 7.2 and 7.4). In addition, 25 radio-tagged chub were stocked at the downstream site only. A further 75 fish of each species, marked only with Alcian blue dye, were also stocked at each of the three stocking locations.

7.2.3 Monitoring

Radio-tagged chub were located daily (between 07:00 and 16:00) from the bank using a hand-operated receiver (Sika model; Biotrack, Wareham, UK) and a three-element Yagi antenna over a four-week period (20 October – 21 November 2005 and 28 October – 1 December 2006). During both study periods, two separate, intensive, 24-hour surveys found both wild and stocked fish to be inactive at night, thus daytime locations were considered representative of overall movement patterns. Tagged fish could be recorded at a distance of up to 200m with the antenna held at head height.

The location of individual fish was determined to within 1m by triangulation from the bank (to avoid disturbing the fish) or more usually by reducing the gain on the receiver to localise the fish from either bank. When fish were located, their position was recorded with reference to riverside features and the type of habitat occupied was noted. Fish locations were subsequently plotted in ArcGIS (ESRI ArcMAP version 9.1) and the distance moved by the fish (to the nearest metre along the river midline) between successive tracking trips was calculated. Habitat use was divided into open water and within complex habitat (instream macrophytes and overhanging and submerged terrestrial vegetation). During the 26–27 November 2006 flood event, specific habitat (such as reed beds) could not be determined because the river was too deep and turbid, but the location within the stream was recorded (deep pool, slack water or backwater).

At the end of the study period in both years, any fish that had not moved for several days were disturbed to ensure they were alive (upstream movement had to be observed) or had not shed their tags or been eaten, especially as pike are abundant in the Roding. Jepsen *et al.* (1998) found radio tags from salmon smolts on the river bed 3–6 days after the smolts had been eaten by pike; a similar effect was assumed to be applicable in this study. Large fish-eating birds were not observed along the study reach in more than 150 hours of observation. Ten radio-tagged wild fish were recaptured using electric fishing in December 2005, but elevated flow during most of the winter in 2006 prevented post-tracking sampling.

Mark-recapture sampling (single run, pulsed DC electric fishing; Bateman *et al.* 2005) was performed on 11–17 March 2006 (Table 7.1) and 19–28 March 2007. All fish were measured (fork length), hand-scanned for PIT tags and examined for Alcian marks. During March 2006, random stratified sampling was performed, ensuring that at least 600m within every 1km of the study river (10km) was sampled in order to minimise sampling bias (Gowan *et al.* 1994).

During March 2007, the whole study reach (except for a few short, inaccessible sections) was sampled (50 sites, mean length (m \pm SD) = 187.7 \pm 63.5), as well as 0.5km upstream of the upstream limit and 1.4km downstream of the study reach. Further to this, three sites were enclosed using stop nets. Each site was fished three times to test sampling efficiency, which was derived from absolute abundance estimates determined from the Maximum Likelihood Methods (Carle and Strub 1978) (Table 7.5).

Table 7.5 Total population (n \pm SE) and probability of capture (P \pm SE) for chub, dace and roach as determined by the Maximum Likelihood Methods (Carle and Strub 1978) for the three sites sampled quantitatively

Site	Total population (n \pm SE)			Probability of capture (P \pm SE)		
	Chub	Dace	Roach	Chub	Dace	Roach
24	-	29 \pm 1	7 \pm 0	-	0.76 \pm 0.14	0.78 \pm 0.24
42	5 \pm 0	-	24 \pm 3	0.83 \pm 0.25	-	0.61 \pm 0.22
47	-	-	62 \pm 3	-	-	0.71 \pm 0.12

The PIT antenna stations were cross-channel swim-through loop antennae, half-duplex systems with 23mm tags (Texas Instruments RFID, 134 kHz; see Zydlewski *et al.* 2001 for further information). Two loops, around 2m apart, were used at a single site, allowing the direction of movement to be recorded. Five dual-loop stations (A1–A5) were installed during the first study period, with an extra station (A6) added before the second study year. PIT stations (A1 to A6) were located 1050m, 3450m, 4550m, 6700m, 8050m and 9150m from the upstream limit of the study section. Site selection was influenced by the river width (<8.0m) and depth (<0.7m), and the availability of bankside access to change batteries.

Each PIT detector interrogated the two loops synchronously at a rate of three times per second with a maximum horizontal range (perpendicular to river cross-section) of 0.6m. The PIT detectors were powered by two 110Ah deep cycle lead-acid batteries connected in parallel, providing at least 14 days of life. Preliminary studies (M.C. Lucas unpublished) showed that this frequency of interrogation, while relatively slow (thus conserving power), detected more than 99.5% of tagged cyprinids passing a single loop, as their swimming and water velocities were normally well under 1 m s^{-1} .

Tag detection data (identity, date, time) for each antenna were stored on a flash memory card housed in the logger unit (Flinka Fiskar, Sweden) and were downloaded onto a portable laptop computer at every battery change. Throughout the study, the effectiveness of each antenna was periodically tested using a tag mounted on the tip of a wooden pole. Efficiency of detection for actual fish was determined from the direction of movement from a known location (tagging location or previous loop record) or from recaptured fish that passed a loop without producing a record. During the first year of study, the average field detection efficiency was 99.0% (Table 7.6). During the second year, loops were unable to sample the full depth of the water column during several high flow events and were not operational 100% of the time (to avoid flooding). Nevertheless, 92.8 % of fish movements were still recorded (Table 7.7).

7.2.4 Output processing and data analysis

Radio tracking

Analysis of the spatial behaviour of radio-tracked chub was based on two descriptors of the pattern and extent of movements: range per day tracked and daily distance. Range per day tracked was calculated by dividing the linear range (the difference between the maximum distance upstream and downstream recorded throughout the tracked period) by the number of days the fish was tracked. This describes the extent of river used, standardised for the period of tracking.

Daily distance for each fish was calculated by dividing the total distance moved (calculated from the position recorded every day) by the period over which the fish was tracked, and reflects the overall level of movement. Differences in mean range per day tracked and mean daily distance between years for wild fish and between wild and stocked fish in 2006 were compared using the Mann Whitney *U*-test. Spearman rank correlation was used to investigate the influence of temperature and flow on the movements of wild and stocked chub.

Habitat use was calculated for each fish as the percentage of tracking events located in either open water or in complex habitat. A chi-squared test was used to test the null hypothesis that habitat use did not differ significantly between wild and stocked fish in 2006. In addition, mean daily distance and habitat use comparisons between wild and stocked fish were made before and after the initial elevated flow period in 2006 (18–19 November). During 2006, three tags in wild fish failed in the period 15–22 November and five tags in stocked fish failed in the period 13–18 November, thus these fish were only included in the analysis of movements prior to the first elevated flow period.

Table 7.6 PIT antenna operational details, downstream, upstream and milling fish movements recorded and missed, and the proportion of movements missed during 2005–06 sampling

	A1	A2	A3	A4	A5
Date installed	14/11/05	06/11/05	05/11/05	05/11/05	05/11/05
Date removed	09/06/06	09/06/06	09/06/06	09/06/06	09/06/06
Days installed	206.8	215.0	215.3	215.7	215.7
% of time operational	100.0	100.0	100.0	100.0	100.0
Downstream					
Recorded	227	148	118	111	37
Not detected (%)	0 (0.0)	2 (1.3)	1 (0.8)	1 (0.9)	1 (2.6)
Upstream					
Recorded	247	151	138	131	69
Not detected (%)	2 (0.8)	4 (2.6)	1 (0.7)	2 (1.5)	1 (1.4)
Milling fish	150	6	23	118	33
Total fish records	624	305	279	360	139
Missed fish (%)	2 (0.3)	6 (1.9)	2 (0.7)	3 (0.8)	2 (1.4)

Mark recapture

A chi-squared test was used to test the null hypothesis that the proportion of radio-tracked chub recaptured did not differ significantly between tagging occasion, followed by the Mann-Whitney *U*-test as a *post hoc* test. Mann-Whitney *U*-tests were also used to test the hypothesis that the proportion recaptured did not differ significantly between species, fish origin (wild/stocked) and stocking location. A *t*-test was performed on the initial fish mass of recaptured and non-recaptured fish, for all species and tag sizes, to test the null hypothesis that there was no influence of size on mortality.

Sampling sites were plotted in ArcGIS (ESRI ArcMAP version 9.1) and the mark-recapture movement distance (to the nearest metre) was calculated from the midpoint of the capture/release site to the midpoint of the recapture site. For each individual recaptured, positive values were assigned to upstream movers and negative values to downstream movers. Movement distance distributions for each species were plotted using 200m classes.

Daily distance moved for each fish was calculated by dividing the total distance moved by the time since last capture. A Mann Whitney U-test was used to compare differences in mean daily distance between years for wild fish and between fish species and origin within each year. A chi-squared test was used to test the null hypothesis that there was no directional bias in fish movements.

Table 7.7 PIT antenna operational details, downstream, upstream and milling fish movements recorded and missed, and the proportion of movements missed during 2006–07 sampling

	A1	A2	A3	A4	A5	A6
Date installed	03/10/06	04/10/06	03/10/06	03/10/06	03/10/06	26/10/06
Date removed	08/05/07	08/05/07	06/05/07	08/05/07	05/05/07	08/05/07
Days installed	216.6	215.9	214.3	216.6	213.9	193.7
Days operational (%)	214.6	211.6	198.0	195.4	208.9	169.0
% of time operational	99.1	98.0	92.4	90.2	97.6	87.3
Downstream						
Recorded	659	559	351	771	378	380
Not detected (%)	54 (7.6)	35 (5.9)	71 (16.8)	123 (13.8)	76 (16.7)	27 (6.6)
Upstream						
Recorded	851	710	308	943	301	301
Not detected (%)	52 (5.8)	36 (4.8)	36 (10.5)	57 (5.7)	34 (10.1)	33 (9.9)
Milling fish	446	279	252	627	249	436
Total fish records	1956	1539	906	2334	928	1097
Missed fish (%)	106 (5.1)	71 (4.4)	107 (10.6)	180 (7.2)	111 (10.6)	60 (5.2)

Fixed station PIT telemetry

The proportion of active individuals for each species was expressed as a proportion of the tagged fish recorded on a PIT antenna. Daily distance moved for each remotely-detected PIT-tagged fish was calculated based on PIT antenna locations, and a Mann Whitney U-test was used to compare movement distances between sampling techniques and years, and fish species and origin. All statistical analyses described above were carried out using SPSS (version 14.0) with a significance level $\alpha = 0.05$.

Generalised Linear Models (GLM) with logratio link function and a negative binomial error function were constructed to examine the influence of environmental factors on fish activity (Genstat, version 10.0; VSN International Ltd, UK). Activity (percentage of known alive fish recorded on the antennae per day) was used as the model response, while flow and temperature were used as the predictors. Full factorial models were initially constructed then the least significant factors were removed.

7.3 Results

Between October 2005 and May 2007, a total of 2814 wild and hatchery reared fish were tagged (Table 7.1), released and monitored using radio telemetry, mark recapture and fixed location PIT telemetry equipment. Large variations in numbers recaptured and movements were identified between species, fish origin and monitoring technique.

7.3.1 Radio tracking

During 2005, just one tag malfunctioned after 13 days. In 2006, however, despite the same tag design being used, 10 of the tags applied to stocked chub failed prior to release. A further three tags in stocked fish and three in wild fish failed within a week of release, thus limiting any further analysis of these fish. Thirty-two wild juvenile chub ($n = 20$ in year 2005 and $n = 12$ in 2006) and 12 stocked chub (2006) were tracked for up to 30 days each year, equating to 1181 daily fish records. All fish recaptured in December 2005 were in good condition and their wounds had begun to heal (not completely healed in some cases because of low temperatures and slight variations in the day tagged), suggesting that any variability in movements and behaviour were not the result of the tagging.

Elevated flow during most of the winter in 2006 prevented post-tracking capture of chub; but there was no reason to suspect any fish died, as all fish with operational tags were still mobile at the end of the study. Additionally, towards the end of the study period, two stocked fish suspected of radio-tag malfunction were recorded moving upstream through a remote PIT antenna (A4) placed 460m upstream of the stocking location and 400m downstream of Fyfield Mill. The 400m section between the antenna and the mill was searched extensively but no signal could be detected, thus validating suspicions of tag malfunction whilst removing concerns of poor signal searching technique by the tracker and/or unrecorded long-range movements from the study reach. In addition, no mortality of wild and stocked cyprinids was observed during the first month after release.

Over both study years, the mean ranges per day tracked (2005 = 6.5m day^{-1} , 2006 = 7.3m day^{-1} : Mann Whitney U -test: $Z = -1.479$, $n = 32$, $P = 0.146$) and mean daily distances (2005 = 12.1m day^{-1} , 2006 = 14.7m day^{-1} : Mann Whitney U -test: $Z = -0.272$, $n = 32$, $P = 0.803$) of radio-tagged wild chub were similar (Figure 7.1). During 2006, radio-tagged stocked chub exhibited significantly larger mean range per day tracked (43.2m day^{-1} : Mann Whitney U -test: $Z = -3.550$, $n = 19$, $P < 0.001$) and mean daily movement (96.7m day^{-1} : Mann Whitney U -test: $Z = -3.467$, $n = 19$, $P < 0.001$) than wild fish (Figure 7.1).

When examined in more detail, daily movements of radio-tagged stocked chub were similar to radio-tagged wild chub at low flows (for the first 15 days after release; Mann Whitney U -test: $Z = -1.914$, $n = 24$, $P = 0.060$), but were significantly larger than radio-tagged wild chub during periods of elevated flow (Mann Whitney U -test: $Z = -3.228$, $n = 16$, $P < 0.001$). For example, during the first elevated flow event of 19 November 2006, five of the seven radio-tagged stocked chub moved at least 725m upstream. During the second elevated flow period of 26–27 November 2006, two radio-tagged stocked chub moved large distances downstream (at least 1990m), but returned to the area of stocking two days later. At the end of the radio tracking period (1 month), all radio-tagged stocked chub were upstream of the stocking location.

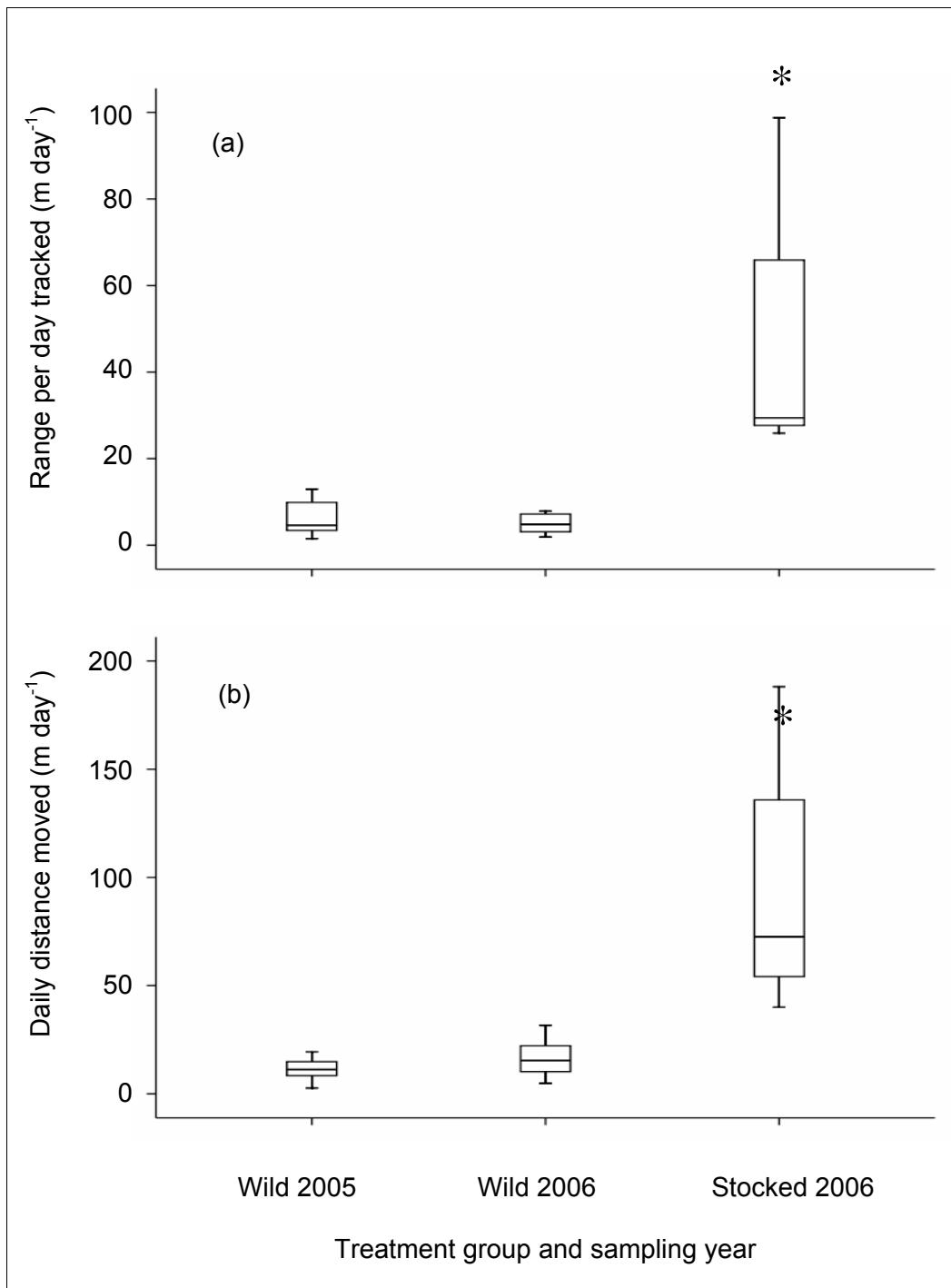


Figure 7.1 (a) Range per day tracked and (b) distance moved per day tracked of chub in the different treatment groups (wild 2005, wild 2006 and stocked 2006)

Note: Box plots represent the 10th, 25th, 50th, 75th and 90th percentiles. * denotes $P < 0.001$ stocked fish movements significantly larger than wild fish.

During 2005, radio-tagged wild chub spent 30.9% of the time swimming around in open water. Comparing habitat use during 2006 revealed that radio-tagged stocked chub spent significantly more time in open water than wild chub (68.2% versus 27.1%; χ^2 with continuity correction = 249.712, d.f. = 1, $P < 0.001$), although differences were less significant under elevated flow later in the tracking period (37.1% versus 17.7%; χ^2 with continuity correction = 5.112, d.f. = 1, $P = 0.024$). During the 26–27 November 2006 flood, both stocked and wild radio-tagged chub occupied deep and wide pools with reduced flow (40% versus 11%) and areas of slack water (created by trees, terrestrial

vegetation or macrophytes; 60% versus 70%), but only wild chub were located in an off-channel backwater (19 %).

7.3.2 Mark recapture

During the March 2007 sampling, 137 wild chub, 116 dace and 140 wild roach were recaptured. Wild fish were tagged on four occasions during the study (Table 7.1), but this had no influence on the subsequent recapture of chub (χ^2 : 12mm PIT = 1.540, d.f. = 3, $P = 0.673$; 23mm PIT = 4.641, d.f. = 3, $P = 0.200$) and roach (χ^2 : 12mm PIT = 1.484, d.f. = 3, $P = 0.686$; 23mm PIT = 0.834, d.f. = 3, $P = 0.841$) (Table 7.8).

Significantly less dace tagged with 12mm PIT in October 2005 were recaptured (Mann Whitney U -test: March 2006: $Z = -2.468$, $n = 47$, $P = 0.014$; October 2006: $Z = -2.581$, $n = 38$, $P = 0.010$), but significantly more dace tagged with 23mm PIT in October 2006 were recaptured (Mann Whitney U -test: October 2005: $Z = -2.007$, $n = 190$, $P = 0.045$; December 2005: $Z = -2.636$, $n = 95$, $P = 0.008$) (Table 7.8).

Table 7.8 Number of chub, dace and roach tagged (n) during each sampling occasion and the proportion recaptured (% (n)) in March 2007

Treatment / Release date	Chub tagged (n)	Recap. % (n)	Dace tagged (n)	Recap. % (n)	Roach tagged (n)	Recap. % (n)
Wild 12mm PIT						
Oct-05	13	38.5 (5)	28	10.7 (3)	91	18.7 (17)
Dec-05	20	30.0 (6)	10	30.0 (3)	52	15.4 (8)
Mar-06	23	47.8 (11)	19	42.1 (8)	18	11.1 (2)
Oct-06	11	45.5 (5)	10	50.0 (5)	69	21.7 (15)
Wild 23mm PIT						
Oct-05	81	40.7 (33)	118	34.7 (41)	215	21.4 (46)
Dec-05	56	57.1 (32)	23	17.4 (4)	49	20.4 (10)
Mar-06	56	44.6 (25)	42	40.5 (17)	48	27.1 (13)
Oct-06	36	55.6 (20)	72	48.6 (35)	130	22.3 (29)
Stocked 23mm PIT						
Nov-06 S1	175	33.7 (59)	-	-	174	57.5 (100)
Nov-06 S2	175	35.4 (62)	-	-	174	58.6 (102)
Nov-06 S3	200	16.0 (32)	-	-	175	36.0 (63)
Stocked Alcian blue control						
Nov-06	225	32.0 (72)	-	-	224	53.6 (120)

The proportion of wild chub (12mm PIT = 40.3 %, 23mm PIT = 48.0 %) recaptured in March 2007 was significantly greater than the proportions of wild roach (12mm PIT = 18.3 %, 23mm PIT = 22.2 %) (Mann Whitney U -test: 12-mm PIT: $Z = -3.846$, $n = 297$, $P < 0.001$; 23-mm PIT: $Z = -6.863$, $n = 671$, $P < 0.001$) and dace tagged with 23mm PIT (38.0 %) (Mann Whitney U -test: $Z = -2.305$, $n = 484$, $P = 0.021$). However, dace were captured significantly more than roach tagged with 23mm PIT (Mann Whitney U -test: $Z = -4.388$, $n = 697$, $P < 0.001$). Fish mass at tagging had no influence on the subsequent recapture of chub (12mm PIT: $t = 0.126$, $P = 0.900$; 23mm PIT: $t = -0.619$, $P = 0.536$), dace (12mm PIT: $t = -1.706$, $P = 0.093$; 23mm PIT: $t = -1.523$, $P = 0.129$) or roach (12mm PIT: $t = -1.612$, $P = 0.113$; 23mm PIT: $t = -0.395$, $P = 0.693$).

Proportionally fewer stocked chub (28.0%) were recaptured in comparison to wild chub (55.6%) (Mann Whitney *U*-test: $Z = -3.561$, $n = 586$, $P < 0.001$), but the opposite was observed for roach (stocked 50.5%, wild 22.3%) (Mann Whitney *U*-test: $Z = -5.606$, $n = 652$, $P < 0.001$) (Table 7.8). Fish mass at tagging had no influence on the subsequent recapture of stocked chub (Mann Whitney *U*-test: $Z = -0.436$, $n = 550$, $P = 0.663$) or roach ($t = -1.864$, $P = 0.063$). A similar proportion of Alcian control stocked fish and 23mm PIT-tagged stocked fish were caught (Mann Whitney *U*-test: chub: $Z = -1.216$, $n = 775$, $P = 0.224$; roach: $Z = -0.990$, $n = 746$, $P = 0.322$), implying that PIT tagging had no influence on the stocked fish recapture rate. In addition, all recaptured fish (including wild fish) were in good condition, with healed tagging sites, suggesting that any variability in movements and behaviour were not the result of tagging.

The proportion of recaptured fish was significantly lower for stocking at site S3 (chub 16.0%, roach 36.0%), the most downstream stocking location, compared with S1 (chub 33.7%, roach 57.5%) (Mann Whitney *U*-test: chub : $Z = -4.115$, $n = 375$, $P < 0.001$; roach: $Z = -4.406$, $n = 348$, $P < 0.001$) and S2 (chub 35.4%, roach 58.6%) (Mann Whitney *U*-test: chub: $Z = -4.452$, $n = 375$, $P < 0.001$; roach: $Z = -4.406$, $n = 348$, $P < 0.001$) (Table 7.8). This is possibly a result of sampling difficulties in the deeper and wider section of river downstream of Fyfield Mill.

Wild fish were exposed to marked differences in temperature and flow between sampling years, but the mark-recapture mean daily distances (total distance moved divided by the time since last capture) for chub were similar for both years (2005–06 = 1.0m day^{-1} , 2006–07 = 4.3m day^{-1} ; Mann Whitney *U*-test: $Z = -1.096$, $n = 65$, $P = 0.273$) (Figure 7.2). Dace (2005–06 = 2.2m day^{-1} , 2006–07 = 6.8m day^{-1} ; Mann Whitney *U*-test: $Z = -3.379$, $n = 89$, $P = 0.001$) and roach (2005–06 = 2.1m day^{-1} , 2006–07 = 3.1m day^{-1} ; Mann Whitney *U*-test: $Z = -2.028$, $n = 79$, $P = 0.043$) moved significantly more in 2006–07, although the movements were mainly upstream (χ^2 : dace = 13.520, d.f. = 1, $P < 0.001$; roach = 4.568, d.f. = 1, $P = 0.033$) (Figure 7.3). However, no PIT-tagged fish were caught upstream of the upper reach limit.

In 2005–06, movements were similar between species ($\chi^2 = 1.139$, d.f. = 2, $P = 0.566$), but in 2006–07 dace moved significantly more than chub (Mann Whitney *U*-test: $Z = -3.389$, $n = 112$, $P = 0.001$) or roach (Mann Whitney *U*-test: $Z = -2.659$, $n = 115$, $P = 0.008$) (Figure 7.2).

During 2006–07, mean daily distance moved calculated using mark-recapture was significantly larger for stocked fish than for wild fish (Mann Whitney *U*-test: chub (9.2m day^{-1}): $Z = -5.667$, $n = 203$, $P < 0.001$; roach (5.3m day^{-1}): $Z = -3.751$, $n = 314$, $P < 0.001$) (Figure 7.2). No differences were found in the distance moved by wild fish of both species, but stocked chub moved significantly further than stocked roach (Mann Whitney *U*-test: $Z = -3.423$, $n = 412$, $P = 0.001$).

At the end of the study period, proportionally more stocked chub (χ^2 : S2 = 20.903, d.f. = 1, $P < 0.001$) and roach (χ^2 : S1 = 43.560, d.f. = 1, $P < 0.001$; S2 = 49.991, d.f. = 1, $P < 0.001$) were upstream of the stocking location (Figure 7.4), despite experiencing flows reaching up to 14.4 times normal flow (14 February 2007). However, significantly more chub stocked at S3 were recaptured downstream ($\chi^2 = 23.516$, d.f. = 1, $P < 0.001$).

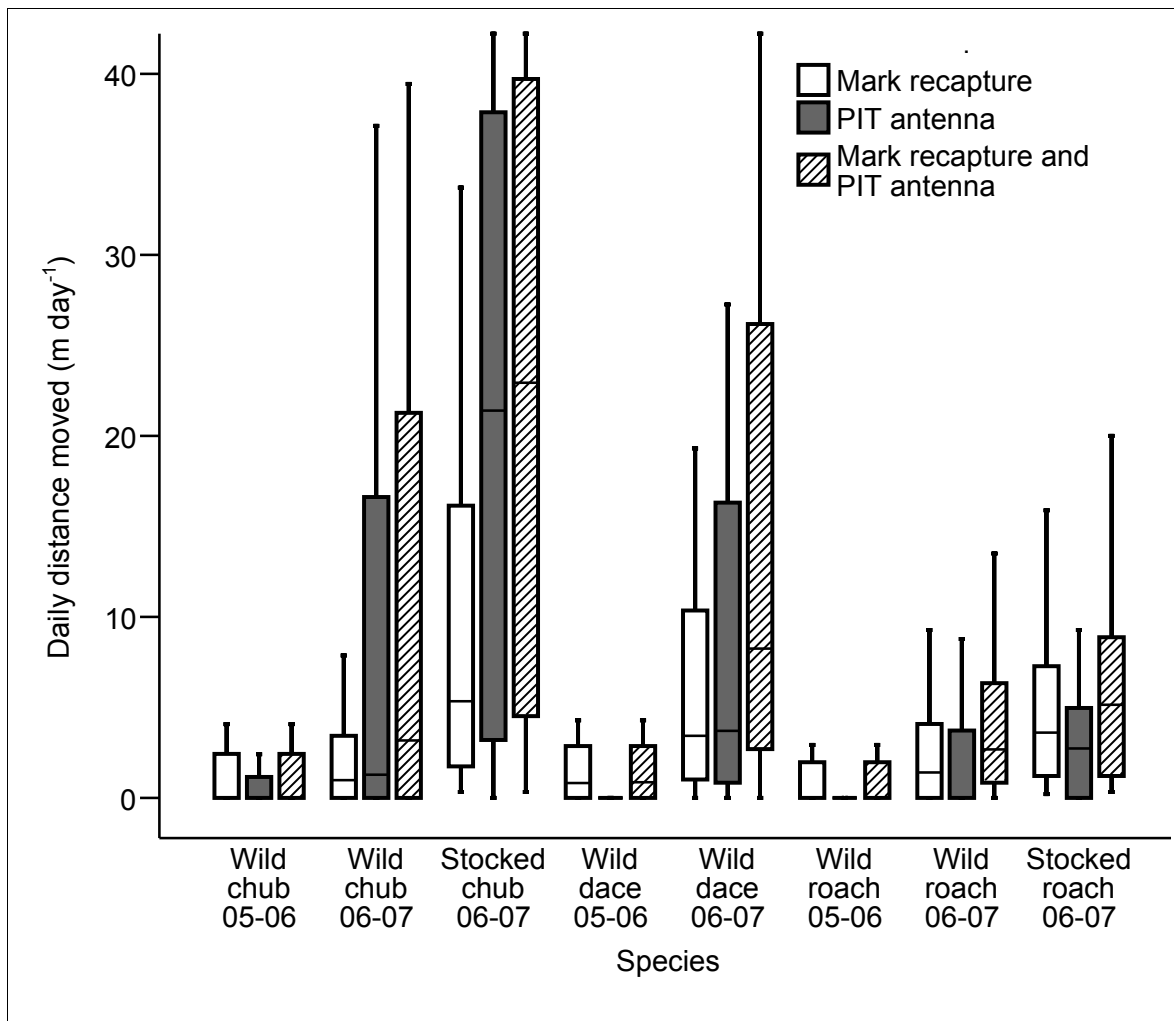


Figure 7.2 Daily distance moved by wild chub, dace and roach (05–06 and 06–07) and stocked chub and roach (06–07), as revealed by mark-recapture, PIT antenna records and a combination of both techniques

Note: Box plots represent the 10th, 25th, 50th, 75th and 90th percentiles; see text for explanation.

7.3.3 Fixed station PIT telemetry

The trends uncovered by mark-recapture were only partially supported by fixed station PIT antenna records. For example, in 2005–06 mark-recapture revealed that the distance moved was similar for all fish species (see above), whereas different species accounted for varying proportions of the fish passing through the antennae (chub = 21.2%, dace = 5.0% and roach = 1.9%). In addition, mark-recapture revealed that the daily distance moved by wild chub and their locations after each winter were similar between years, whereas proportionally more fish were found to move through the PIT antennae during 2006–07 (chub = 21.2% and 48.8%).

This finding suggests that more wild chub moved during 2006–07, but that they subsequently returned to the area local to tagging. Similarly, proportionally more dace (5.0% and 57.3%) and roach (1.9% and 29.0%) moved during 2006–07. However, the proportions of wild fish moving through PIT loops were small (chub 48.8%, roach 29.0%) compared with stocked chub (91.6%) and roach (58.1%).

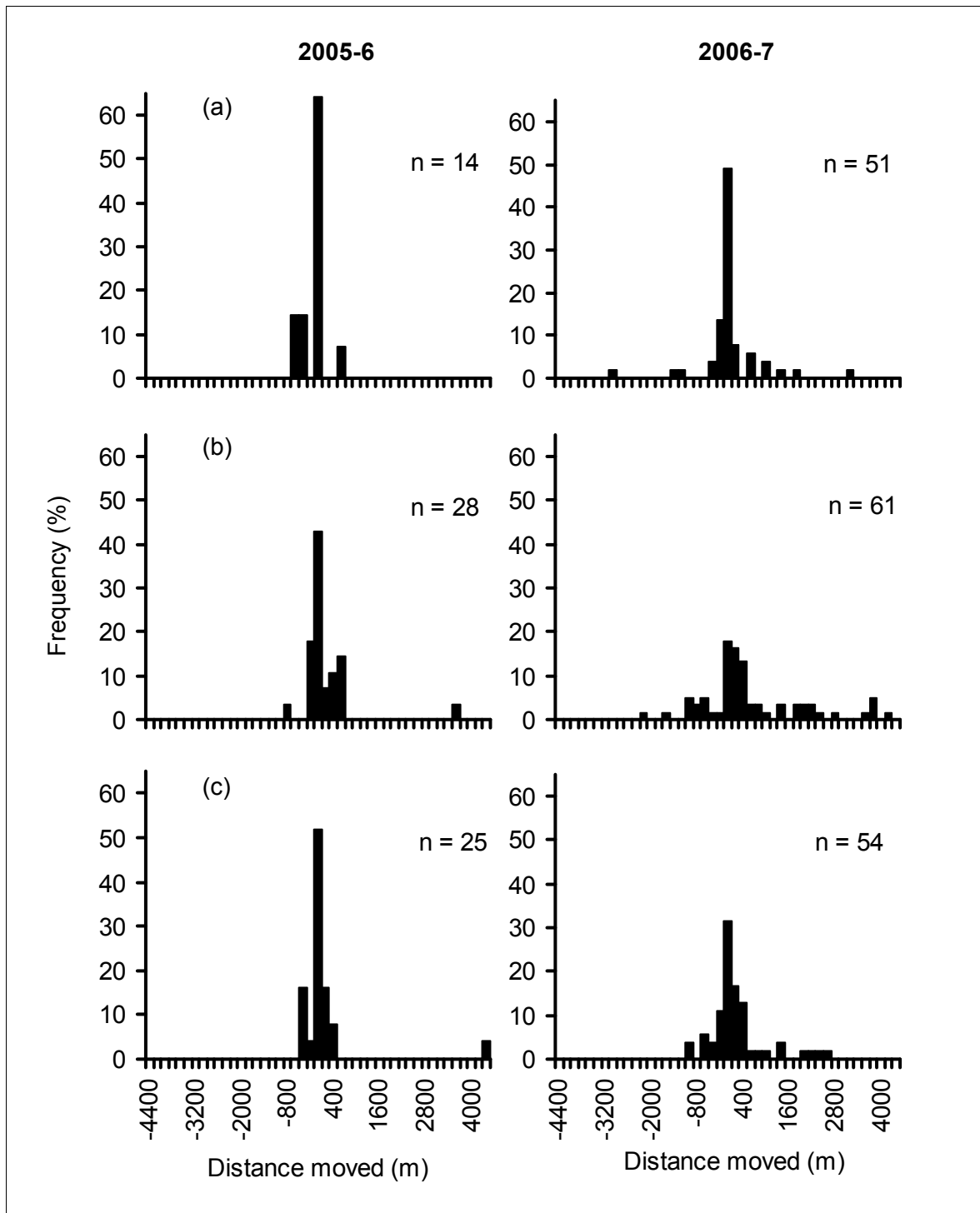


Figure 7.3 Range of dispersal (mark-recapture) (m) of PIT-tagged wild (a) chub, (b) dace and (c) roach from October 2005 – March 2006 and October 2006 – March 2007

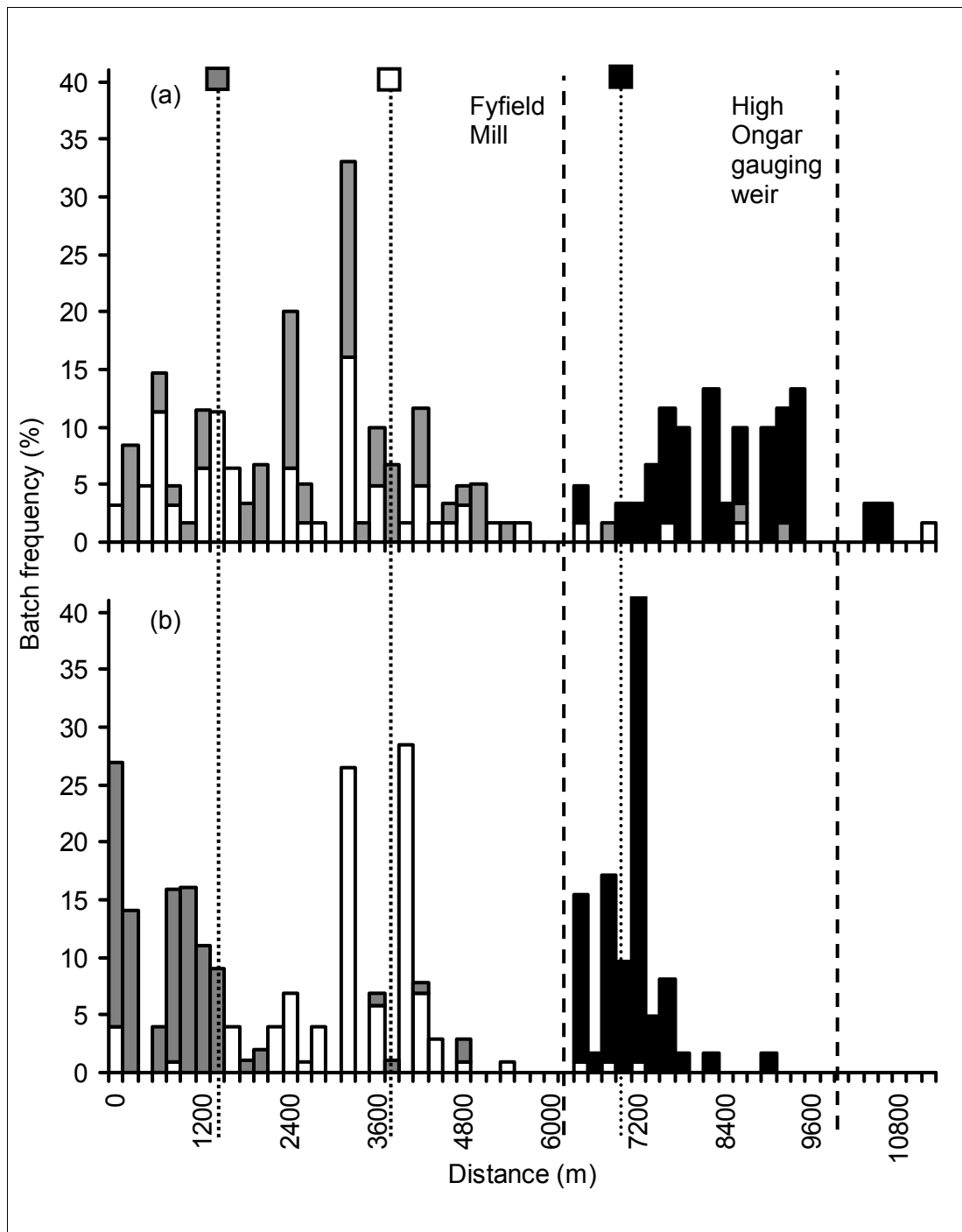


Figure 7.4 Stocking locations (fine dashed line: S1, ■; S2, □; and S3, ■) and recapture distribution (batch frequency (%)) of (a) chub and (b) roach
 Note: Thick dashed lines represent the location of Fyfield Mill and High Ongar gauging weir.

Large differences in the distances moved by fish were also found between mark-recapture and PIT antenna records for individual species within years (Figure 7.2). During 2005–06, fish moved relatively short distances and hence rarely moved through PIT antennae, although average daily movements (chub = 0.9m day⁻¹, dace = 0.7m day⁻¹, roach = 0.4m day⁻¹) based on mark-recapture were significantly higher (Mann Whitney *U*-test: chub: $Z = -0.848$, $n = 129$, $P = 0.396$; dace: $Z = -4.372$, $n = 89$, $P < 0.001$; roach: $Z = -4.940$, $n = 117$, $P < 0.001$). However, the maximum distances moved by an individual PIT-tagged chub, dace and roach were 3080m, 3380m and 4450m, based on PIT antenna records.

During 2006–07, wild fish moved greater distances and passed more antennae. In consequence, the daily distances moved based on PIT antenna records (chub = 10.9m day⁻¹, dace = 10.8m day⁻¹, roach = 2.9m day⁻¹), were significantly greater than recorded the previous winter for all wild fish (Mann Whitney *U*-test: chub: $Z = -4.086$, $n = 135$, $P < 0.001$; dace: $Z = -7.810$, $n = 119$, $P < 0.001$; roach: $Z = -5.776$, $n = 124$, $P < 0.001$). The maximum distances moved by individual wild chub (11,350m) and dace (9630m) were considerable, but the largest distance moved by an individual wild roach was 2050m based on PIT antenna records.

Thus, during 2006–07, PIT antennae recorded more wild fish on loops and greater daily distances moved than during 2005–06, but the distributions of wild fish were similar between years (Figure 7.3). For although PIT antennae often recorded widespread back and forth movements during periods between marking and recapture, fish were often recaptured not far from the last capture. Consequently, for those fish that were recaptured, calculating distance moved between release and recapture locations, combined with PIT antenna records, provides a better estimate of movement during the study, for both relatively sedentary (roach) and mobile (chub and dace) species (Figure 7.2).

The daily distances moved by PIT-tagged stocked chub (21.3m day⁻¹) recorded on PIT antennae were significantly greater than those found using mark-recapture (Mann Whitney *U*-test: $Z = -4.180$, $n = 304$, $P < 0.001$). They were also significantly greater than the daily movements of PIT-tagged wild chub recorded on PIT antennae (Mann Whitney *U*-test: $Z = -3.748$, $n = 195$, $P < 0.001$). Movements of individual PIT-tagged stocked chub were also far larger than wild chub movements, reaching a maximum gross distance of 25,535m (measured at the resolution of PIT detector separation). Nevertheless, the stocked chub tended to remain in the study area.

Unlike stocked chub, PIT-tagged stocked roach (3.0m day⁻¹) moved relatively little, meaning that distances calculated from PIT antenna records were significantly smaller than those calculated from mark-recapture (Mann Whitney *U*-test: $Z = -6.920$, $n = 520$, $P < 0.001$). But their movements were similar to those of wild roach calculated from PIT antenna records (Mann Whitney *U*-test: $Z = -0.976$, $n = 293$, $P = 0.329$).

Large variations in the number of PIT-tagged fish detected on antennae per day were found for all species of wild fish in both years (Figure 7.5). During 2005–06, movements of wild chub were significantly influenced by river flow (GLM: deviance = 8.28, d.f. = 111, residual deviance = 28.86, $P(\chi^2) = 0.004$), whereas dace and roach activity was more influenced by river temperature (GLM: dace: deviance = 14.26, d.f. = 111, residual deviance = 20.56, $P(\chi^2) < 0.001$; roach: deviance = 4.14, d.f. = 111, residual deviance = 20.62, $P(\chi^2) = 0.042$). Wild fish activity in 2006–07 was driven by a combination of flow and temperature for all species of wild fish (GLM: chub: deviance = 5.38, d.f. = 145, residual deviance = 34.89, $P(\chi^2) = 0.020$; GLM: dace: deviance = 4.56, d.f. = 145, residual deviance = 37.67, $P(\chi^2) = 0.033$; roach: deviance = 5.54, d.f. = 145, residual deviance = 37.70, $P(\chi^2) = 0.019$).

Despite large variations in flow, the daily directions of fish movements were never significantly different for chub ($P > 0.05$): on each day the numbers of fish moving in an upstream direction were similar to the numbers moving downstream. Only on day 48 (0.8m³/s) were the numbers of fish moving downstream significantly greater for dace ($\chi^2 = 4.455$, d.f. = 1, $P = 0.035$), while for roach this happened on days 63 (1.3m³/s: $\chi^2 = 6.400$, d.f. = 1, $P = 0.011$) and 137 (2.0m³/s: $\chi^2 = 4.571$, d.f. = 1, $P = 0.033$). However, this movement was not under the influence of elevated flow; fish were not washed downstream while the PIT antennae were operational. On day 161 (12/03/2006) significantly more PIT-tagged dace moved upstream through the antennae ($\chi^2 = 6.545$, d.f. = 1, $P = 0.011$).

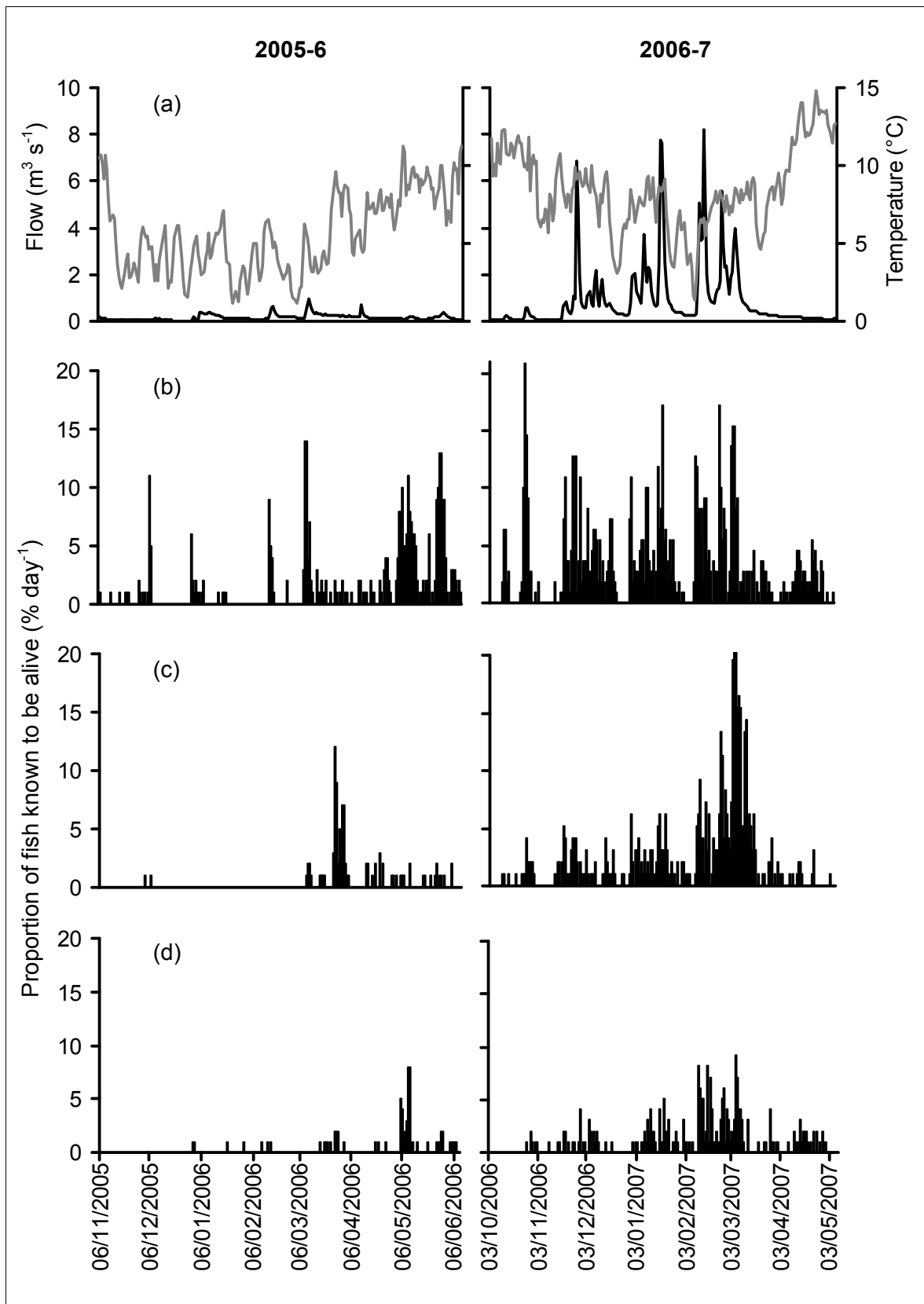


Figure 7.5 (a) Flow ($\text{m}^3 \text{s}^{-1}$) and temperature ($^{\circ}\text{C}$) compared with the daily detections (proportion of fish known to be alive (% day $^{-1}$)) of (b) wild chub, (c) wild dace and (d) wild roach during 2005–06 and 2006–07 sampling periods

The daily activity of stocked chub and roach was not significantly influenced by any combination of factors (GLM: $P > 0.05$), although variations in activity were observed through the sampling period (Figure 7.6). A large proportion of stocked chub, but not wild chub or stocked roach, were recorded on PIT antennae during the first two days after release. During the first two periods of elevated flow (18–19 November and 26–27 November 2006; up to 14.2 times normal flow), stocked chub and roach moved extensively (Figure 7.6). Although the daily directions of stocked fish movements were not significantly different during this period ($P > 0.05$), large numbers of stocked chub (56) moved downstream through A6, with 40% subsequently returning to the area upstream of A6.

Proportionally more stocked fish moved during the first six weeks after release (chub = 64.0% and roach = 53.5% of all movements detected), meaning that recorded movements of stocked fish were far less during subsequent periods of elevated flow. The movements of stocked PIT-tagged chub for the first 30 days after release were significantly influenced by river flow (GLM: deviance = 4.06, d.f. = 118, residual deviance = 22.47, $p(\chi^2) = 0.044$). But no combination of factors significantly influenced stocked PIT-tagged roach for up to the first six weeks after release (GLM: $P > 0.05$).

7.4 Discussion

The combination of sampling techniques employed in this study allowed identification of the spatial distributions, and temporal patterns of movement and habitat use of wild and stocked cyprinids. Wild fish distribution (mark-recapture) after each winter was similar between years, but radio telemetry and fixed location PIT telemetry revealed that significantly more wild fish moved in the second winter, correlated with environmental influences (temperature and flow).

During the second year of the study, PIT-tagged stocked fish moved extensively during the period just after release (radio telemetry and PIT antennae) and the final distributions (mark-recapture) were more dispersed than observed for wild fish. To maximise the success of river improvement schemes and future stocking activities, these variations are now considered in relation to existing knowledge of wild and stocked fish movement.

7.4.1 Wild fish movements

At the end of both winters, recaptured marked wild cyprinids had high levels of 'site fidelity' (Spencer *et al.* 1990) and only a few fish moved large distances (leptokurtically distributed). These findings support previous mark-recapture studies that documented restricted movements of stream fish during non-migratory periods, although the population does contain a small proportion of 'mobile' fish that perform long range movements (Stott 1967; Gowan *et al.* 1994; Hilderbrand and Kershner 2000; Skalski and Gilliam 2000; Nakamura *et al.* 2002; Rodriguez 2002). Other studies have similarly described strong site fidelity of chub (Allouche *et al.* 1999; Penczak 2006), dace (Clough and Beaumont 1998) and roach (Stott 1967; Williams 1965; Baade and Fredrich 1998). Even Linfield (1985) stated that cyprinids lack a home range in large lowland rivers, but concluded that they did over-winter in specific habitats. Consequently, the high site fidelity displayed by the species studied in the River Roding may be to an over-wintering home range.

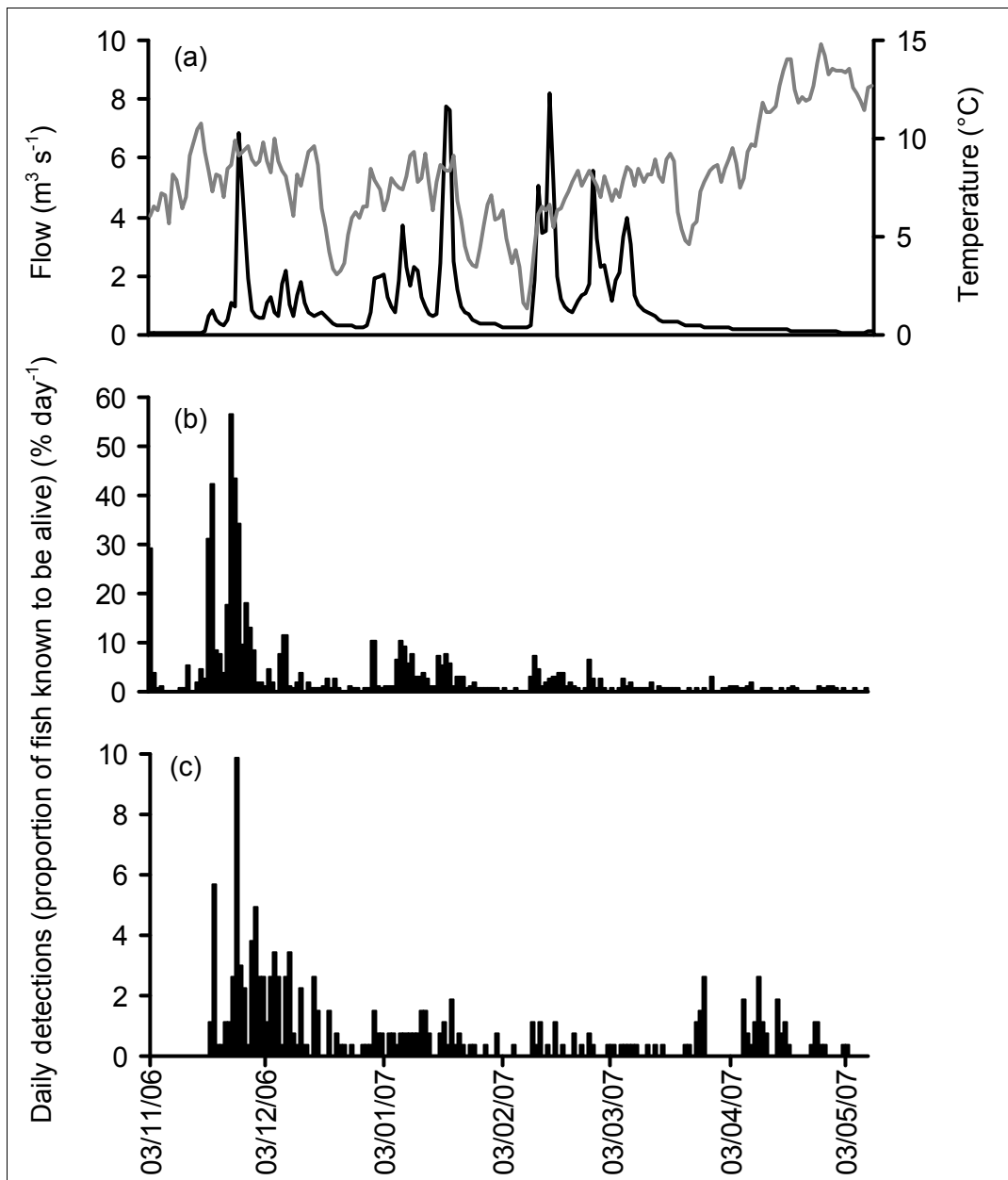


Figure 7.6 (a) Flow (m^3/s) and temperature ($^{\circ}\text{C}$) compared with the daily detections (proportion of fish known to be alive that were detected ($\% \text{ day}^{-1}$)) of (b) stocked chub and (c) stocked roach during 2006–07 sampling period

Radio tracking and PIT telemetry permitted analysis of fish movement over finer temporal scales than was possible with mark-recapture studies, and provided an insight into the behavioural mechanisms associated with movements. Wild fish activity and movements were influenced by temperature and flow, an observation regularly reported for the migratory movements of temperate river fishes (Lucas and Baras 2001). During the first year of study, cold winter temperatures and low flows persisted throughout the winter. As a result, movements were restricted due to cold temperatures reducing metabolism, feeding and swimming, whilst increasing the need to conserve energy.

Furthermore, wild fish tended to occupy areas of habitat complexity, possibly to avoid predation from pike, which were abundant in the Roding study reach (fish-eating birds were quite rare). The predation threat during low flows may cause fish to shelter and reduce movement, thus reducing the probability of encountering a predator (Allouche

and Gaudin 2001; Fraser *et al.* 2006). The benefits of moving (improved feeding or shelter) need to be weighed against the cost of movement. However, it should be noted that Gilliam and Fraser (2001) found that movement rates increased with exposure to a predation threat.

Sections of river may also be less hospitable or more resistant to movement, such as possessing longer riffles (Lonzarich *et al.* 2000; Schaefer 2001) or a shallower depth (Aparicio and Sostoa 1999). However, fish in the Roding were capable of moving past such potential barriers. Crook (2004) reported that fish occasionally move large distances because of predator interactions or reduced habitat quality during winter, or for exploratory purposes.

During the second study year, greater ranges of flow and temperature occurred. The movements of radio-tagged stocked chub were limited in both years, even during elevated flows (26–27 November 2006), as the fish occupied areas of complex habitat, slack waters, wider and deeper pools with reduced flow, and off-channel areas. Other studies reported similar habitat use during elevated flows (Pearsons *et al.* 1992; Allouche *et al.* 1999).

The limited movements of radio-tagged fish are probably a reflection of the small sample size, because the data from the PIT antenna revealed that proportionally more wild fish moved during the second study year, with individual wild fish also moving significantly greater distances. This finding supports the assessment that individual cyprinid behaviour appears to be temporally variable and characterised by 'switching' (Harcup *et al.* 1984). Numerous studies report that fish are capable of switching between sedentary and long-range movement behaviours (Smithson and Johnston 1999; Hilderbrand and Kershner 2000; Knaepkens *et al.* 2004; Crook 2004).

The fish moved during elevated flows (both up and down stream), perhaps because increased depth and turbidity reduced the potential exposure to predation. Dispersal success may be higher if the animal chooses to disperse under safer conditions (Zollner and Lima 2005). We do not know the definitive reasons for such movements, but the fish may have been performing exploratory movements for feeding (Gowan *et al.*, 1994; Smithson and Johnston, 1999; Albanese *et al.* 2004) or to find habitat for refuge (Brown *et al.* 2001). They may even have simply been searching to gain knowledge (Gowan and Fausch 2002), as stream fish can explore and exploit at great distances.

Mark-recapture fish distributions were comparable at the end of each winter. However, the fish moved extensively during the second study winter, suggesting a strong site fidelity by homing to the initial tagging location. Site fidelity and homing has been reported in cyprinids for diel feeding (Clough and Ladle 1997), spawning (Fredrich *et al.* 2003), after displacement by high flows (Lucas 2000), and following translocation experiments (Stott 1967; Crook 2004). Kramer and Chapman (1999) suggested fish return to original home ranges after displacement because of the costs associated with learning a new home range.

Homing of fish could involve a combination of several learnt aspects of specific locations, including odours and landmarks (Odling-Smee and Braithwaite 2003). Some fish did not show fidelity to the initial tagging location (home range shift). This is possibly because of individual differences in ability (sensory or physiological) and/or motivation to return to the initial home range, physical alterations to the initial home range during elevated flow, and/or the availability of suitable or even superior habitat elsewhere in the river (Crook 2004). Alternatively, fish may have been outside their home range at the time of tagging.

7.4.2 Stocked fish movements

In the River Roding, large numbers of PIT-tagged stocked chub moved considerable distances in the first two days immediately after release, with radio-tagged stocked chub largely occupying open water. Evidence from wild fish suggests it is preferable to restrict movements and occupy areas of habitat complexity during low flows. Such variations in movement and behaviour between wild and stocked fish are considered a consequence of genetic differences (local adaptation of stocks), domestication (rearing environments influencing development and learning) and/or acclimatisation to the new environment (reviewed by Weber and Fausch 2003).

Notwithstanding this, stocked fish movements were not within or between habitat patches: fish moved long distances past numerous areas of available and suitable habitat. Thus, stocked fish probably moved to assess the suitability of potential residence areas prior to settling into home ranges (habitat exploration; Crook 2004). Exploratory behaviour for stocked chub (rheophilic species) was more extensive than for stocked roach (eurytopic species), probably because of the more specific habitat requirements of the former. Armstrong *et al.* (1997) reported that most transplanted Atlantic salmon settled in to new home ranges after a short period (<2.5 days) of exploratory behaviour in an experimental stream channel. Following these exploratory movements and subsequent settlement, movements of stocked fish in the Roding were minimal during low flows.

During the initial elevated flow periods (18–19 November and 26–27 November 2006; up to 14.2 times normal flow), radio-tagged stocked chub were found occupying local areas of habitat complexity or marginal vegetation (Pearsons *et al.* 1992; Schwartz and Herricks 2005), although large numbers of stocked fish (radio and PIT telemetry) moved both up- and downstream. As suggested for wild fish, stocked fish probably moved for exploratory purposes, using areas of low flow associated with marginal vegetation to minimise energy expenditure.

Although a large number of stocked chub moved downstream during the first elevated flow period, with similar behaviour also reported for salmonids (Bettinger and Bettoli 2002), a large proportion (40%) quickly returned to the area local to stocking, possibly suggesting a homing ability in stocked fish. This conclusion is further supported by the limited movement of stocked fish during subsequent elevated flow periods, suggesting the development of site fidelity. However, validation of this hypothesis was not possible, because the location of the home range after initial exploratory movements was not established. More important from a stocking perspective was the finding that stocked cyprinids have the behavioural and physiological ability to cope with elevated flows, a concern previously raised for salmonids (MacDonald *et al.* 1998) and cyprinids (Cowx *et al.* 1986). In addition, nearly all the recaptured stocked fish remained in the reach depleted by the pollution event.

Despite the majority of recaptured fish remaining in the target section of the river, the timing and extent of stocked chub movement had possible consequences for their survival. Aprahamian *et al.* (2004) reported substantially higher loss rates for stocked cyprinids than for wild populations, although that study was methodologically flawed, as detailed earlier. We found no evidence for the reduced survival of stocked radio-tagged chub, but the increased activity and long range movements of PIT-tagged stocked chub probably did expose the fish to increased predation (Sparrevohn *et al.* 2002; Henderson and Letcher 2003; Aarestrup *et al.* 2005). It may also have ultimately resulted in greater energy expenditure, which may have reduced long-term survival (Hurst 2007).

Thus, based on the lower recapture rate of stocked chub, high rates of exploration and movement may not be advantageous traits for stocked cyprinids establishing in new locations. In addition, stocked roach were largely recaptured in shoals with wild fish

(authors' personal observations), thus diluting the individual predation threat (Pitcher and Parrish 1993) and allowing predator-naïve fish to learn anti-predator responses from experienced wild fish (Brown and Smith 1998; Kelley and Magurran 2003). Similarly, predator exposure and experience after release could have induced predator recognition and avoidance behaviour (Kelley and Magurran 2003), thus explaining why stocked fish reduced their movements during the study.

This study employed several methods to determine the dispersal, behaviour and fate of stocked cyprinids in more detail than had been achieved previously. At face value, it found that stocked fish demonstrated markedly higher persistence within the vicinity of the stocking area than reported by previous studies. Assuming a recapture efficiency of 0.7 (see Table 7.1), a mean recapture of stocked chub of 28% translates to 40% persistence, while a mean recapture of stocked roach of 51% translates to 73% persistence after an over-winter period of five months, including several high-flow events.

Although the study was carried out at one river and for a limited period only, the results suggest that stocked fish do not necessarily experience very high mortality rates, nor are they washed out of the stocking area by high flows, provided that habitat structure is good. The short-term results appear particularly good for roach, with chub displaying wider dispersal but also (on the basis of recaptures) lower survival. These results do not suggest that hatchery rearing and stocking of fish is a pointless exercise, although there may be ways of enhancing its effectiveness.

7.4.3 Experimental considerations

Although variable rates of stocked fish recapture were found, directly influenced by the amount of movement, recapture rates of wild roach were particularly low, despite limited movements. Low recapture rates of fish could have several causes, such as low tag retention, mortality, sampling escapement or fish moving out of the study area (Gowan *et al.* 1994). Laboratory trials prior to the field study reported 100% tag retention and no negative effects of tagging on the survival or growth of roach similar in size to those tagged during the field study (Chapter 6). Electric fishing is known to cause stress (Bracewell *et al.* 2004) and injuries (Synder 2003) to fish. However, Skov *et al.* (2005) reported that electric fishing and tagging (23mm PIT without sutures, as in this study) had no effects on the condition or survival of similar-sized roach in both laboratory and field investigations. Furthermore, wild chub and dace were subjected to the same experimental procedure and displayed better recapture rates than wild roach.

It is therefore considered most likely that wild roach were perhaps more difficult to catch, because of greater electric fishing avoidance or because their preferred habitat was more difficult to sample (deep pools or dense vegetation). Ultimately, the recapture rates were comparable to other studies describing the movement of stream fishes (for example, 26% in Hill and Grossman 1987; 8% and 20% in Freeman 1995), suggesting that mortality or low sampling efficiency have not biased the conclusions (Roberts and Angermeier 2007).

Gowan *et al.* (1994) suggested that the findings of many historic studies of fish movements were undermined by insufficient sampling of long-range movements out of study sections. In this study on the River Roding, a 14km stretch of river was sampled, suggesting that most tagged fish that were not recaptured either died or were missed by the electric fishing. This suggestion is further supported by the PIT antennas, which documented the medium-term movements of large samples of individual small fish past certain locations within the study reach.

Without PIT antenna technology, the movement of fish from the study section could have been interpreted as mortality and returning fish would have been interpreted as

not moving. For example, Jonsson *et al.* (1999) concluded that mark-recaptured stocked brown trout caught in the area of stocking did not actively search for new habitats after introduction, but the low temporal resolution of the mark-recapture technique meant that this conclusion could not be confirmed. Furthermore, had a combination of full-reach resampling and continuous telemetry not been carried out, it would have been easy to suggest that stocked cyprinid fish persistence was low (*cf.* Barnard *et al.* 2002; Aprahamian *et al.* 2004). By applying the approach of Aprahamian *et al.* (2004), we would have obtained much poorer measures of stock fish persistence (chub = 9% and roach = 25%), because the inadequate spatial distribution of the sampling process is unable to resolve highly aggregated populations.

This issue is critical for the Environment Agency, since our data raise strong doubts about the reliability of the Environment Agency's previous attempts to measure the fate of stocked cyprinid fishes. Such data are critical for the economic evaluation of the utility of stocking. Although limited to one river and study period, our data suggest that the net retention, and hence value, of stocked fish is likely to be higher than may previously have been considered.

7.5 Conclusions

By employing three different monitoring techniques (radio tracking, mark-recapture and fixed station PIT telemetry) over two years, we were able to obtain detailed and precise spatial and temporal information on fish distribution and movements in relation to environmental factors. Specifically, the high sampling effort and cross-calibration of information demonstrated the markedly higher persistence of stocked chub and especially stocked roach than found in previous Environment Agency studies.

The highly aggregative behaviour and elevated mobility that may be displayed by cyprinids (as exemplified in this study) are likely to increase markedly any bias inherent in measuring persistence by mark-recapture methods alone. Evidence from mark-recapture revealed similar distributions of wild fish between years, suggesting restricted movement of the fish, although the populations comprised both residents and mobile fish. However, data from fixed location PIT telemetry during the second study year found that wild fish were actually far more active, performing extensive movements (exploratory, exploitation or refuge) when exposed to more variable environmental influences (flow and temperature). By considering individual movements at suitable spatial and temporal scales and using a combination of techniques, a more complete understanding of wild cyprinid ecology and general stream fish movement was obtained. The results provide evidence of variations in behaviour in response to relatively natural flow regimes (Poff *et al.*, 1997), and illustrate the necessity for protecting and restoring longitudinal connectivity.

After the second study winter, stocked fish were more widely distributed than wild fish. Furthermore, their movements were more extensive than those of wild fish and the movements of stocked chub were not correlated to abiotic factors. Specifically, PIT telemetry identified the following behaviour in stocked fish: exploratory movements immediately after stocking; large numbers of fish moving during the first flood; the return of displaced fish; reduced movements of stocked fish with time; and the large total distances stocked fish moved during the five months after release.

Genetic and phenotypic factors (review in Weber and Fausch 2003) are regularly cited as explanations for stocked fish behaviours, but we believe our understanding of stocked fish behaviour has been enhanced by considering their movements in relation to simultaneous studies of wild fish. In this study, although most of the stocked fish remained in the stream section local to stocking, extensive movements of stocked chub

appear to have had direct consequences on survival, a vital measure of stocking success.

Future efforts to improve post-release behavioural performance of chub and other stocked cyprinids could include environmental enrichment (Braithwaite and Salvanes 2005) and life skills training (Brown and Laland 2001). Greater attention also needs to be given to the influence of existing stock density and the resultant competition among fish, as well as to the influence of environmental factors at the time of release on stock fish survival and dispersal. The common timing for release is in the autumn, when annual growth is near complete and when husbandry conditions allow grading and transport of fish with minimal mortality. Although other options for the timing of release may exist, this study suggests that high flow events occurring soon after stocking in autumn do not necessarily compromise the survival and persistence of stocked cyprinids.

8 General discussion

8.1 Introduction

The movements and dispersal of cyprinid fish, in both lateral and longitudinal directions, are strongly influenced by flow. In lowland reaches, floods are characterised by lateral expansion onto floodplains. This results in high levels of aquatic habitat heterogeneity, which is essential for fish refuge, spawning, nursery and feeding (Chapter 2). However, in rivers subject to anthropogenic disturbance to floodplain connectivity, floods have detrimental effects on 0+ fish populations (Chapter 3). Thus, there is a need to restore and rehabilitate lowland rivers in order to try to recover natural features or functionality.

In rivers where man-made floodplain waterbodies have recreated functional habitats, lateral connectivity is important for both juvenile (Chapter 4) and adult fish (Chapter 5). Marking and tracking of individual cyprinids (Chapter 6) allows improved understanding of the influence of temperature and flow on the longitudinal movements of both wild and stocked sub-adult cyprinids (Chapter 7). The overall aim of this study was to examine the factors influencing the lateral and longitudinal dispersal of juvenile and adult (wild and stocked) cyprinid fish in lowland rivers and to ascertain the influence of elevated flows on these respective communities. To this end, the study was divided into key topics that are addressed in Chapters 2 to 7. This chapter integrates and discusses the knowledge gained from the previous six chapters, drawing key conclusions and providing recommendations for further study.

8.1.1 Lateral dispersal of fish

Chapter 2 provided a review of how natural floodplains in lowland rivers have high structural diversity, which is not only maintained but is often increased by erosional and depositional processes during floods. Freshwater fish species have evolved different life history strategies, which are classified according to where particular species spawn along the lotic-to-lentic succession of habitat that occurs both downstream of rivers and along lateral directions. Even the larvae and juveniles of strictly rheophilic species such as dace and gudgeon disperse from river spawning grounds and use floodplain habitats as nurseries. Floodplain habitats also provide essential locations for young progeny to take refuge during floods, primarily because of their poor swimming capabilities.

Anthropogenic disconnection of floodplains from the river can have adverse consequences for fishes, during both elevated and normal flow conditions. The isolation of rivers from their floodplains is of particular importance during floods. This is because it can lead to increased severity of conditions in the main river channel, prevent fish from seeking refuge in floodplain habitats and leave fish stranded when artificial levees are 'over-topped'. During floods of varying timing and magnitude in the Yorkshire Ouse, backwaters provided refuge for high densities of 0+ eurytopic fishes, with gudgeon and other strictly rheophilic species also captured on a regular basis. However, rheophilic fishes were rarely stranded on the floodplain (Chapter 3).

Peak fish densities on the floodplain occurred during the summer (August), despite there being floods of higher magnitude during the winter. Thus, floods can cause mortality of 0+ fish if they occur soon after spawning. Furthermore, samples of fish taken from rivers immediately after floods contained significantly larger bleak and roach

than pre-flood samples, suggesting small fish were more susceptible to displacement and/or mortality.

Rehabilitation efforts should reinstate lateral and longitudinal connectivity by restoring a more natural hydrologic regime and recreating functional habitats (recovery towards a 'normative' condition). In the River Trent, local and overall species diversity, richness, turnover and the guild composition of fish communities in 10 man-made floodplain waterbodies were influenced by variable hydrological connectivity to the river. This broad spectrum of connectivity produced habitats similar to a natural riverscape, with fish assemblages comparing favourably with studies on unmodified river reaches. The lotic-to-lentic succession of habitat from the main river channel into the floodplain corresponded to a sequence of rheophilic-to-eurytopic-to-limnophilic fish species. This study provides support for incorporating man-made floodplain waterbodies of variable, not just high, levels of hydrological connectivity into holistic riverine ecosystem management plans.

DIDSON was used to provide fine-resolution, non-interventional information on adult fish movements between the Yorkshire Ouse and a permanently-connected, man-made floodplain waterbody (a marina) under normal and elevated flow (Chapter 5). The largest and most consistent variations in movements in the connecting channel were between day and night samples, with fish being much more active and present at higher densities during the day. The diurnal variations were considered most likely to be a trade-off between foraging and avoiding piscivorous birds, particularly cormorants, in the main river.

Increased river flow resulted in significantly reduced fish movements, both in and out of the marina, and reduced fish presence at the entrance. This result is contrary to the findings from other studies and is possibly a result of the fish finding localised refuge (at the bottom or margins of the marina) from elevated flows within the main river. However, lateral movements may still occur during higher flow events, when conditions are more severe in the main channel.

8.1.2 Longitudinal movements of fish

Longitudinal movements of small cyprinids (both wild and stocked) have been little studied, partly because of monitoring limitations. Although there have been numerous studies on the suitability of VIE or PIT tags for fishes, especially salmonids, few have determined the most reliable and appropriate long-term marking techniques for cyprinids. It is shown in Chapter 6 that VIE implantation can provide a cheap, batch-marking technique, as long as retention rates are monitored. However, PIT tags are recommended as the most suitable method for tagging individual juvenile chub, dace and roach, based on the high retention, low fish mortality and minimal growth effects. Specifically, small cyprinids (>9cm fork length) can be tagged with 12mm PIT tags, while slightly larger fish (>12cm fork length) can be tagged with 23mm tags. Although the use of 12mm PIT tags would be preferred for mark-recapture purposes, given their negligible recorded effects on fish health, the range advantages of 23mm PIT tags for telemetry applications (Lucas and Baras 2000; Zydlewski *et al.* 2001) probably outweigh any minor effects on growth.

The combination of PIT and radio telemetry employed in the River Roding study allowed identification of the habitat use, spatial distribution and temporal movements of individual wild and stocked cyprinids (Chapter 7). The mark-recapture distribution of wild cyprinids at the end of both winters suggested that they largely had high levels of 'site fidelity', but that highly mobile individuals were also present within the population. Radio-tracking revealed that wild chub tended to occupy areas of habitat complexity,

whilst PIT telemetry revealed that wild cyprinid behaviour was temporally variable, correlated with temperature and flow.

Habitat use and movements are probably related to energy expenditure, metabolic capacity, feeding and predation threat. During elevated winter flows, wild fish occupied areas of reduced flow. Since feeding and metabolic capacity are low at this time of the year, we interpret this as an attempt to reduce energy expenditure. However, some fish performed exploratory movements under the influence of increased depth and turbidity (reduced predation), possibly because of reduced habitat quality over the winter or in order to find flow refuge. Despite extensive movements, some fish returned to their initial tagging site.

PIT telemetry and radio-tracking revealed that movements of stocked fish were more frequent and larger than for wild fish, particularly in the period soon after release. This movement was possibly for exploratory purposes. Subsequently, movements of stocked fish were minimal and did not correlate with flow or temperature, with the final distributions more dispersed than observed for wild fish. The persistence of stocked roach and chub compared very favourably with other studies and suggests hatchery-rearing and stocking of cyprinids can be successful, at least in the short term. However, had a combination of full-reach scale re-sampling and continuous telemetry not been carried out, it would have been easy to suggest that stocked cyprinid fish persistence was low (*cf. Aprahamian et al. 2004*).

An important finding from a stocking perspective is that stocked cyprinids had the behavioural and physiological ability to cope with elevated flows and mostly remained in the section of river affected by the pollution event. Nevertheless, further trials are needed to investigate issues such as the optimum conditions for performance training to flows, the persistence of stocked cyprinids in relation to size of batch stocked and the density of fish existing in the receiving water. Differences in habitat use between wild and stocked chub were observed, and the timing and extent of stocked chub movement probably had consequences for their survival, a vital measure of stocking success. The influence of such factors may help to explain the mechanisms behind the differential mortality between wild and stocked fish, and might suggest improvements that can be made to husbandry prior to stocking.

8.2 Conclusions and recommendations

8.2.1 Lateral movements

Backwaters can provide refuge for high densities of 0+ fishes, including eurytopic and strictly rheophilic species during flood events. **It is recommended that backwater areas are constructed on channelised rivers for fish refuge during high flows, especially in sections of river where it is not possible to reconnect floodplains.** Specifically, altering channel morphology and encouraging riparian vegetation (trees, bushes and dense reeds) of sufficient height and strength to deflect flow will create areas of slack water at high flows, with inevitable benefits for a large proportion of the 0+ fish population.

Large numbers of 0+ fish were stranded and died on floodplains behind 'over-topped' levees, especially after summer floods. **It is recommended that levees should be set back as far as feasibly possible and be designed so that ditches and channels allow all the water to drain back into the river. Furthermore, water should be able to return to the river quickly (as flood waters recede) in order to reduce potential mortality from piscivorous birds, low dissolved oxygen and high levels of**

tannins. In areas where flood levees must remain, but are still liable to ‘over-topping’, water drainage structures such as flap-gates are encouraged, whilst sluices and pumps should be avoided because they are likely to cause physical damage or even mortality to fish during operation. If pumps have to be used, defences should be employed to prevent entry of fish or to divert fish to refuges elsewhere. By following these guidelines, these kinds of managed floodplain areas will provide refuge for fish during elevated flows and safe egress back to the river as flood waters recede. It is also important to recognise the flood protection benefits to society provided by the natural functional attributes of floodplain landscapes.

Both adult and juvenile fish made use of man-made floodplain waterbodies. The findings of this study should be explicitly incorporated into plans for lowland river rehabilitation and floodplain restoration. **It is recommended that man-made floodplain waterbodies with variable connectivity should be excavated where anthropogenic activities have reduced floodplain habitats.** Such waterbodies recreate functional habitats for spawning, feeding, nursery (growth) and resting (self-protection), thereby improving the status of fish populations in degraded rivers. Such efforts are integral to the UK’s obligations under the WFD to improve the ecological status of rivers. Importantly, these restoration strategies do not focus on a single taxonomic group or species. Such restoration or rehabilitation efforts may only be necessary for limited reaches in order to maintain the fishery and biodiversity (the ‘string of beads principle’; Cowx and Welcomme 1998). However, future research efforts should aim to identify the required frequency and size of such habitats so as to provide maximum benefits to biodiversity.

DIDSON provided fine-resolution information about the lateral movements of fish in a connection channel between a lowland river and a connected floodplain waterbody, an environment where current sampling techniques have inherent problems. **It is recommended that future investigations of lateral movements specifically incorporate DIDSON technology, whilst also attempting to verify the numbers, species and size composition of imaged fish.** By doing so, a far greater understanding of the importance of floodplain waterbodies for adult fish will be gleaned.

The movement of juvenile and adult fish between the main river channel and floodplain waterbodies is a complex process, involving spawning, foraging, predator avoidance and flow refuge behaviours. Furthermore, lunar cycles (Gaudreau and Boisclair 2000), temperature (Lilja *et al.* 2003) and turbidity (Jepsen and Berg 2002) can all potentially influence the movements, activity patterns and habitat use of fish. **It is recommended that future investigations should monitor lateral movements over both finer (such as diel) and longer (such as seasonal) time scales, in an attempt to elucidate species-specific timings and environmental influences on such movements. These investigations should also include an analysis of stomach contents over 24-hour periods.** Such efforts could employ DIDSON, as well as traps for juvenile fish and tags for adult fish, whilst measuring detailed water quality variables (suspended solids, ammonia and the distribution of food items) in both the main river channel and the floodplain waterbody. Ideally these studies should be replicated at the same site under similar conditions. Where possible, the methodology should be applied across multiple sites and rivers to determine the degree to which observed patterns are generic to lowland river systems.

8.2.2 Tag retention trials

Variations in survival rates, mark retention and growth rates between species over the duration of the laboratory experiment emphasised the importance of long-term mark feasibility trials for the species under study. **It is recommended that future tagging investigations are species-specific and of sufficient duration to determine the**

most reliable and appropriate long-term marking technique. Such efforts will validate field results, helping to determine if recaptures of marked fish are representative of unmarked populations and whether recapture rates are reduced by low survival of marked fish or poor retention of marks.

During the laboratory tagging investigation, fish were not exposed to the same stresses as encountered in a natural environment (predation, density, and feeding), thus survival and growth may have been artificially elevated in the controlled setting. This possibility is perhaps most relevant for dace, which is most sensitive to capture and handling out of the three species studied, with a higher incidence of scale loss and fin damage. **It is recommended that future tagging trials incorporate predation and growth experiments under field conditions, but in a 'controlled' environment, such as managed outdoor ponds.** Specifically, experiments should test the effects of anaesthesia, tagging and transportation on growth and survival. Such trials would reduce concerns about high field variability and remove issues of variable sampling efficiency in the field.

Differences in recapture rates between wild fish were considered to be a consequence of electric fishing avoidance and/or habitat use variations between species, but these differences could also be attributed to capture and tagging procedures. Furthermore, hatchery-reared fish were not exposed to electric fishing and were tagged two weeks prior to stocking, due to the large numbers being handled, allowing them to recover from any immediate tagging effects. **It is recommended that future field studies should attempt to quantify the individual and combined effect of electric fishing, handling, anaesthesia and tagging on wild fish.** Such trials would further validate the ecological conclusions drawn from field studies. However, the extended timescale and repeatable behaviour of the wild fish strongly suggest that any differences discovered between wild fish and stocked fish were a reflection of inherent differences in behaviour rather than methodological effects.

8.2.3 Longitudinal movements and stocked fish persistence

By employing different monitoring techniques (mark-recapture, PIT telemetry and radio-tracking), this study obtained detailed and precise spatial and temporal information on fish movements in relation to environmental variables. Without such careful spatial and temporal stratification of wild fish and the post-release monitoring of stocked freshwater fish, it is easy to form erroneous interpretations of their fate. **It is recommended that future studies on individual fish movements and the fate of stocked fish should be considered at an appropriate spatial and temporal resolution, using the correct combination of techniques (similar to the methodology described in this study).** By doing so, such studies will provide a clearer understanding of the movement and survival of stream fish, as well as general fish ecology, and possibly a greater insight into the species-specific variations observed in this study.

Radio-tagged wild (and stocked) chub occupied areas of habitat complexity (instream macrophytes and overhanging and submerged terrestrial vegetation) at all river levels, possibly to avoid predation and to reduce energy expenditure. Additionally, PIT telemetry identified extensive movements during elevated flow. On the basis of radio tracking of chub, these movements are suggested to have occurred in areas of low flow (marginal vegetation) to minimise energy expenditure. **It is recommended that lowland river rehabilitation efforts include recognition of the importance of habitat diversity for juvenile and stocked cyprinids in winter conditions.** Such efforts will help to conserve stream fish populations, especially in relation to the predicted increases in flood frequency and magnitude in response to climate change.

The findings of this study address concerns about the susceptibility of both stocked and wild juvenile cyprinids to displacement during high flows, demonstrating that stocked fish in particular were able to cope with high-flow events. Furthermore, all species of wild fish surveyed occasionally performed long range movements correlated with temperature and flow. **It is recommended that natural flow regimes and longitudinal connectivity are protected and restored.** It is important to recognise the significance of long-range movements for individual fish, but also the influence of these movements on the distribution and abundance of a population, with genetic and evolutionary consequences.

Although most of the stocked fish remained in the stream section local to stocking, behavioural differences (movements and habitat use) between wild and stocked chub were prevalent throughout the study, and probably had consequences for their survival (ultimate measure of success). These differences in behaviour may be the result of genetic differences (local adaptation of stocks), domestication (rearing environments influencing development and learning), acclimatisation to the new environment (reviewed by Weber and Fausch 2003) and/or issues relating to home range. **It is recommended that future studies should determine the factors affecting stocked cyprinid behaviour post-release and quantify such differences in relation to survival.** Specifically, efforts should be made to reduce the effects of domestication through environmental enrichment (Braithwaite and Salvanes 2005) and life skills training (Brown and Laland 2001). Greater attention also needs to be given to the influence of existing stock density and the resultant competition, as well as to the effects of environmental factors at the time of release. Such efforts will inevitably improve the success of future riverine fish stock enhancement measures.

The findings of this study provide an important insight into the movements and fate of stocked cyprinid fish in the winter months immediately after release and make clear some of the inadequacies of previous attempts to obtain this information. **It is recommended that future studies on non-salmonid stocked fish should continue to compare their behaviour to that of wild fish, about which there is a paucity of information.** Specifically, studies should extend over longer periods (including spawning). They should also ideally include comparisons between rivers with different habitat complexity, hydrology and morphology, including both longitudinal and lateral connectivity.

References

- AARESTRUP, K., JEPSEN, N., KOED, A. AND PEDERSEN, S., 2005. Movement and mortality of stocked brown trout in a stream. *Journal of Fish Biology*, 66, 721–728.
- AARTS, B.G.W. AND NIENHUIS, P.H., 2003. Fish zonations and guilds as the basis for assessment of ecological integrity of large rivers. *Hydrobiologia*, 500, 157–178.
- AARTS, B.G.W., VAN DEN BRINK, F.W.B. AND NIENHUIS, P.H., 2004. Habitat loss as the main cause of the slow recovery of fish faunas of regulated large rivers in Europe: The transversal floodplain gradient. *River Research and Applications*, 20, 3–23.
- ADAMS, N.S., RONDORF, D.W., EVANS, S.D. AND KELLY, J.E., 1998. Effects of surgically and gastrically implanted radio transmitters on growth and feeding behaviour of juvenile Chinook salmon. *Transactions of the American Fisheries Society*, 127, 128–136.
- ADAMS, S.R., ADAMS, G.L. AND HOOVER, J.J., 2003. Oral grasping: a distinctive behavior of cyprinids for maintaining station in flowing water. *Copeia*, 2003, 851–857.
- ADAMS, S.R., HOOVER, J.J. AND KILLGORE, K.J., 1999. Swimming endurance of juvenile pallid sturgeon, *Scaphirhynchus albus*. *Copeia*, 1999, 802–807.
- AGOSTINHO, A.A. AND ZALEWSKI, M., 1995. The dependence of fish community structure and dynamics on floodplain and riparian ecotone zone in Paraná River, Brazil. *Hydrobiologia*, 303, 141–148.
- AGOSTINHO, A.A., GOMES, L.C. AND ZALEWSKI, M., 2001. The importance of floodplains for the dynamics of fish communities of the upper River Paraná. *Ecohydrology and Hydrobiology*, 1, 209–217.
- AGOSTINHO, A.A., THOMAZ, S.M., MINTE-VERA, C.V. AND WINEMILLER, K.O., 2000. Biodiversity in the high Paraná River floodplain. In: Gopal, B., Junk, W.J. and Davis, J.A., eds. *Wetlands biodiversity*. Leiden, the Netherlands: Backhuys Publishers, 89–118.
- ALABASTER, J.S. AND ROBERTSON, K.G., 1961. The effect of diurnal changes in temperature, dissolved oxygen and illumination on the behaviour of roach (*Rutilus rutilus* (L.)), bream (*Abramis brama* (L.)) and perch (*Perca fluviatilis* (L.)). *Animal Behaviour*, IX, 187–192.
- ALABASTER, J.S., 1970. River flow and upstream movement and catch of migratory salmonids. *Journal of Fish Biology*, 2, 1–14.
- ALBANESE, B., ANGERMEIER, P.L. AND DORAI-RAJ, S., 2004. Ecological correlates of fish movement in a network of Virginia streams. *Canadian Journal of Fisheries and Aquatic Sciences*, 61, 857–869.
- ALEXANDER, R.M., 1966. Physical aspects of swim bladder function. *Biological Review*, 41, 141–176.
- ALLEN, K.R., 1951. The Horokiwi Stream: A study of a trout population. *New Zealand Marine Department Fisheries Bulletin*, 10, 1–231.
- ALLOUCHE, S. AND GAUDIN, P., 2001. Effects of avian predation threat, water flow and cover on growth and habitat use by chub, *Leuciscus cephalus*, in an experimental stream. *Oikos*, 94, 481–492.
- ALLOUCHE, S., THEVENET, A. AND GAUDIN, P., 1999. Habitat use by chub (*Leuciscus cephalus* L., 1766) in a large river, the French Upper Rhone, as determined by radiotelemetry. *Archiv für Hydrobiologie*, 145, 219–236.
- AMOROS, C. AND BORNETTE, G., 2002. Connectivity and biocomplexity in waterbodies of riverine floodplains. *Freshwater Biology*, 47, 761–776.
- AMOROS, C. AND PETTS, G.E., eds., 1993. *Hydrosystemes fluviaux*. Paris: Masson.
- AMOROS, C., 1991. Changes in side-arm connectivity and implications for river system management. *Rivers*, 2, 105–112.

- AMOROS, C., 2002. Connectivity and biocomplexity in waterbodies riverine floodplains. *Freshwater Biology*, 47, 761–776.
- AMOROS, C., RICHARDOT-COULET, M. AND PAUTOU, G., 1982. Les 'ensembles fonctionnels: des entités écologiques qui traduisent l'évolution de l'hydrosystème en intégrant la géomorphologie et l'anthropisation (exemple du Haut-Rhône français). *Revue de Géographie de Lyon*, 57, 49–62.
- AMUNDSEN, P.A., GABLER, H.M. AND STALDVIK, F.J., 1996. A new approach to graphical analysis of feeding strategy from stomach contents data – modification of the Costello (1990) method. *Journal of Fish Biology*, 48, 607–614.
- APARICIO, E. AND DE SOSTOA, A., 1999. Pattern of movements of adult *Barbus haasi* in a small Mediterranean stream. *Journal of Fish Biology*, 55, 1086–1095.
- APRAHAMIAN, M.W., BARNARD, S. AND FAROOQI, M.A., 2004. Survival of stocked Atlantic salmon and coarse fish and an evaluation of costs. *Fisheries Management and Ecology*, 11, 153–163.
- ARMSTRONG, J.D. AND HERBERT, N.A., 1997. Homing movements of displaced stream dwelling brown trout. *Journal of Fish Biology*, 50, 445–449.
- ARMSTRONG, J.D., BRAITHWAITE, V.A. AND RYCROFT, P., 1996. A flat-bed passive integrated transponder antenna array for monitoring behaviour of Atlantic salmon parr and other fish. *Journal of Fish Biology*, 48, 539–541.
- ARNDT, S.K.A., CUNJAK, R.A. AND BENFEY, T.J., 2002. Effect of summer floods and spatial–temporal scale on growth and feeding of juvenile Atlantic salmon in two New Brunswick streams. *Transactions of the American Fisheries Society*, 131, 607–622.
- ARNOLD, G.P., WEBB, P.W. AND HOLFORD, B.H., 1991. The role of the pectoral fins in station-holding of Atlantic salmon parr (*Salmo salar* L.). *Journal of Experimental Biology*, 156, 625–629.
- ARRINGTON, D.A. AND JEPSEN, D.B., 2001. Evaluation of ecosystem enhancement using growth rates of Centrarchid fishes. *Florida Scientist*, 64, 197–215.
- ARRINGTON, D.A. AND WINEMILLER, K.O., 2004. Organization and maintenance of fish diversity in shallow waters of tropical floodplain rivers. In: WELCOMME, R. AND PETR, T., eds. *Proceedings of the second international symposium on the management of large rivers for fisheries: Volume II*. Bangkok, Thailand: FAO Regional Office for Asia and the Pacific, 25–36, (RAP Publication 2004/17).
- ARSCOTT, D.B., TOCKNER, K., VAN DER NAT, D. AND WARD, J.V., 2002. Aquatic habitat dynamics along a braided alpine river ecosystem (Tagliamento River, NE-Italy). *Ecosystems*, 5, 802–814.
- ARTHINGTON, A.H. AND PUSEY, B.J., 2003. Flow restoration and protection in Australian rivers. *River Research and Applications*, 19, 1–19.
- ARTHINGTON, A.H., BALCOMBE, S.R., WILSON, G.A., THOMS, M.C. AND MARSHALL, J., 2005. Spatial and temporal variation in fish-assemblage structure in isolated waterholes during the 2001 dry season of an arid-zone floodplain river, Cooper Creek, Australia. *Marine and Freshwater Research*, 56, 25–35.
- ARTHINGTON, A.H., RALL, J.L., KENNARD, M.J. AND PUSEY, B.J., 2003. Environmental flow requirements of fish in Lesotho rivers using the DRIFT methodology. *River Research and Applications*, 19, 641–666.
- ASTORGA, N., AFONSO, J.M., ZAMORANO, M.J., MONTERO, D., OLIVA, V., FERNANDEZ, H. AND IZQUIERDO, M.S., 2005. Evaluation of visible implant elastomer tags for tagging juvenile gilthead seabream (*Sparus auratus* L.); effects on growth, mortality, handling time and tag loss. *Aquaculture Research*, 36, 733–738.
- AXFORD, S., 1974. Movement of roach – Hammerton fishery. In: *Roach investigations: part one*. Yorkshire River Authority, 68–56.
- BAADE, U. AND FREDRICH, F., 1998. Movement and pattern of activity of the roach in the River Spree, Germany. *Journal of Fish Biology*, 52, 1165–1174.

- BAILEY, R.E., IRVINE, J.R., DALZIEL, F.C. AND NELSON, T.C., 1998, Evaluations of visible implant fluorescent tags for marking coho salmon smolts. *North American Journal of Fisheries Management*, 18, 191–196.
- BAIN, M.B., FINN, J.T. AND BOOKE, H.E., 1988. Streamflow regulation and fish community structure. *Ecology*, 69, 382–392.
- BALON, E.K., 1975. Reproductive guilds of fishes: a proposal and definition. *Journal of the Fisheries Research Board of Canada*, 32, 821–864.
- BANKS, J.W., 1969. A review of the literature on the upstream migration of adult salmonids. *Journal of Fish Biology*, 1, 85–136.
- BARAS, E. AND LUCAS, M.C., 2001. Impacts of man's modifications of river hydrology on the migration of freshwater fishes: a mechanistic perspective. *Ecohydrology and Hydrobiology*, 1, 291–304.
- BARAS, E. AND NINDABA, J., 1999a. Diel dynamics of habitat use by riverine young-of-the-year *Barbus barbatus* and *Chondrostoma nasus* (Cyprinidae). *Archiv für Hydrobiologie*, 146, 431–448.
- BARAS, E. AND NINDABA, J., 1999b. Seasonal and diel utilisation of inshore microhabitats by larvae and juveniles of *Leuciscus cephalus* and *Leuciscus leuciscus*. *Environmental Biology of Fishes*, 56, 183–197.
- BARAS, E. AND WESTERLOPPE, L., 1999. Transintestinal expulsion of surgically implanted tags by African catfish *Heterobranchus longifilis* of variable size and age. *Transactions of the American Fisheries Society*, 128, 737–746.
- BARAS, E., MALBROUCK, C., HOUBART, M., KESTEMONT, P. AND MELARD, C., 2000. The effect of PIT tags on growth and physiology of age-0 cultured Eurasian perch *Perca fluviatilis* of variable size. *Aquaculture*, 185, 159–173.
- BARAS, E., NINDABA, J. AND PHILIPPART, J.C., 1995. Microhabitats use in a 0+ rheophilous cyprinid assemblage: quantitative assessment of community structure and fish density. *Bulletin Francais de la Peche et la Pisciculture*, 337/338/339, 241–247.
- BARAS, E., WESTERLOPPE, L., MÉLARD, C., PHILIPPART, J. C. AND BÉNECH, V., 1999. Evaluation of implantation procedures for PIT tagging juvenile Nile tilapia. *North American Journal of Aquaculture*, 61, 246–251.
- BARKO, V.A., HERZOG, D.P. AND O'CONNELL, M.T., 2006. Response of fish assemblages to floodplain connectivity during and following a 500-year flood event in the unimpounded upper Mississippi River. *Wetlands*, 26, 244–257.
- BARNARD, S., ANDREWS, K. AND ELLIS, J., 2002. *Optimum stocking strategies for hatchery-reared riverine coarse fish*. Bristol: Environment Agency, (R&D Technical Report).
- BARTOŠOVÁ, Š. AND JURAJDA, P., 2001. A comparison of 0+ fish communities in borrow pits under different flooding regime. *Folia Zoologica*, 50, 305–315.
- BARTOŠOVÁ, Š., JURAJDA, P. AND ONDRAČKOVÁ, M., 1999. Posthodiplostomosis of 0+ juvenile cyprinid fish. *Helminthologia*, 36, 123–136.
- BATEMAN, D.S., GRESSWELL, R.E. AND TORGENSEN, C.E., 2005. Evaluating single-pass catch as a tool for identifying spatial pattern in fish distribution. *Freshwater Ecology*, 20, 335–345.
- BAYLEY, P.B., 1991. The flood pulse advantage and the restoration of the river-floodplain systems. *Regulated Rivers*, 6, 75–86.
- BAYLEY, P.B., 1995. Understanding large river-floodplain ecosystems. *Bioscience*, 45, 153–158.
- BELL, E., DUFFY, W.G. AND ROELOFS, T.D., 2001. Fidelity and survival of juvenile coho salmon in response to a flood. *Transactions of the American Fisheries Society*, 130, 450–458.
- BETTINGER, J.M. AND BETTOLI, P.W., 2002. Fate, dispersal, and persistence of recently stocked and resident rainbow trout in a Tennessee tailwater. *North American Journal of Fisheries Management*, 22, 425–432.

- BISCHOFF, A. AND WOLTER, C., 2001. The flood of the century on the River Oder: Effects on the 0+ fish community and implications for floodplain restoration. *Regulated Rivers: Research and Management*, 17, 171–190.
- BONNEAU, J.L., THUROW, R.F. AND SCARNECCHIA, D.L., 1995. Capture, marking, and enumeration of juvenile bull trout and cutthroat trout in small, low-conductivity streams. *North American Journal of Fisheries Management*, 15, 563–568.
- BORCHERDING, J., BAUERFELD, M., HINTZEN, D. AND NEUMANN, D., 2002. Lateral migrations of fishes between floodplain lakes and their drainage channels at the Lower Rhine: diel and seasonal aspects. *Journal of Fish Biology*, 61, 1154–1170.
- BRACEWELL, P., COWX, I.G. AND UGLOW, R.G., 2004. Effects of handling and electrofishing on plasma glucose and whole blood lactate of *Leuciscus cephalus*. *Journal of Fish Biology*, 64, 65–71.
- BRAITHWAITE, V.A. AND SALVANES, A.G.V., 2005. The importance of environmental variability for coastal cod reared for the rehabilitation of wild populations. *Proceedings of the Royal Society of London, Series B*, 272, 1107–1113.
- BRENNAN, N.P., LEBER, K.M., BLANKENSHIP, H.L., RANSIER, J.M. AND DE BRULER, R., 2005. An evaluation of coded wire and elastomer tag performance in juvenile common snook under field and laboratory conditions. *North American Journal of Fisheries Management*, 25, 437–445.
- BRENNER, T., BUIJSE, A.D., LAUFF, M., LUQUET, J.F. AND STAUB, E., 2003. The present status of the River Rhine with special emphasis on fisheries development. In: WELCOMME, R. AND PETR, T., eds. *Proceedings of the second international symposium on the management of large rivers for fisheries: Volume I*. Bangkok, Thailand: FAO Regional Office for Asia and the Pacific, 121–148, (RAP Publication 2004/16).
- BROWN, A.G., 2002. Learning from the past: palaeohydrology and palaeoecology. *Freshwater Biology*, 47, 817–829.
- BROWN, C. AND LALAND, K., 2001. Social learning and life skills training for hatchery reared fish. *Journal of Fish Biology*, 59, 471–493.
- BROWN, G.E. AND SMITH, R.J.F., 1998. Acquired predator recognition in juvenile rainbow trout (*Oncorhynchus mykiss*): conditioning hatchery-reared fish to recognize chemical cues or a predator. *Canadian Journal of Fisheries and Aquatic Sciences*, 55, 611–617.
- BROWN, L.R. AND FORD, T., 2002. Effects of flow on the fish communities of a regulated California river: implications for managing native fishes. *River Research and Applications*, 18, 331–342.
- BROWN, R.S., COOKE, S.J., ANDERSON, W.G. AND MCKINLEY, R.S., 1999. Evidence to challenge the “2% rule” for biotelemetry. *North American Journal of Fisheries Management*, 19, 867–871.
- BROWN, R.S., POWER, G. AND BELTAOS, S., 2001. Winter movements and habitat use of riverine brown trout, white sucker and common carp in relation to flooding and ice break-up. *Journal of Fish Biology*, 59, 1126–1141.
- BROWN, T.G. and HARTMAN, G.F., 1988. Contribution of seasonally flooded lands and minor tributaries to the production of coho salmon in Carnation Creek, British Columbia. *Transactions of the American Fisheries Society*, 117, 546–551.
- BRUYNDONCX, L., KNAEPKENS, G., MEEUS, W., BERVOETS, L. AND EENS, M., 2002. The evaluation of passive integrated transponder (PIT) tags and visible implant elastomer (VIE) marks as new marking techniques for the bullhead. *Journal of Fish Biology*, 60, 260–262.
- BUIJSE, A.D., COOPS, H., STARAS, M., JANS, L.H., VAN GEEST, G.J., GRIFT, R.E., IBELINGS, B.W., OOSTERBERG, B.W. AND ROOZEN, F.C.J.M., 2002. Restoration strategies for river floodplains in large lowland rivers in Europe. *Freshwater Biology*, 47, 889–907.

- BUNN, S.E. AND ARTHINGTON, A.H., 2002. Basic principles and ecological consequences of altered flow regimes for aquatic biodiversity. *Environmental Management*, 30, 492–507.
- BUZBY, K. AND DEEGAN, L., 1999. Retention of anchor and passive integrated transponder tags by arctic grayling. *North American Journal of Fisheries Management*, 19, 1147–1150.
- CALS, M.J.R., POSTMA, R., BUIJSE, A.D. AND MARTEIJN, E.C.L., 1998. Habitat restoration along the River Rhine in The Netherlands: putting ideas into practice. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 8, 61–70.
- CARLE, F.L. AND STRUB, M.R., 1978. A new method for estimating population size from removal data. *Biometrics*, 34, 621–630.
- CARLINE, R.F. AND MCCULLOUGH, B.J., 2003. Effects of floods on brook trout populations in the Monongahela National Forest, West Virginia. *Transactions of the American Fisheries Society*, 132, 1014–1020.
- CASTRO-SANTOS, T., HARO, A. AND WALK, S., 1996. A passive integrated transponder (PIT) tag system for monitoring fishways. *Fisheries Research*, 28, 253–261.
- CATTANEO, F., LAMOUREUX, N., BREIL, P. AND CAPRA, H., 2002. The influence of hydrological and biotic processes on brown trout (*Salmo trutta*) population dynamics. *Canadian Journal of Fisheries and Aquatic Sciences*, 59, 12–22.
- CHISHOLM, I.M. AND HUBERT, W.A., 1985. Expulsion of dummy transmitters by rainbow trout. *Transactions of the American Fisheries Society*, 114, 766–767.
- CLAIREAUX, G. AND LEFRANÇOIS, C., 1998. A method for the external attachment of acoustic tags on roundfish. *Hydrobiologia*, 371/372, 113–116.
- CLOSE, T.L. AND JONES, T.S., 2002. Detection of visible implant elastomer in fingerling and yearling rainbow trout. *North American Journal of Fisheries Management*, 22, 961–964.
- CLOSE, T.L., 2000. Detection and retention of postocular visible implant elastomer in fingerling rainbow trout. *North American Journal of Fisheries Management*, 20, 542–545.
- CLOUGH, S. AND BEAUMONT, W.C.R., 1998. Use of miniature radio-transmitters to track the movement of dace, *Leuciscus leuciscus* (L.) in the River Frome, Dorset. *Hydrobiologia*, 371/372, 89–97.
- CLOUGH, S. AND LADLE, M., 1997. Diel migration and site fidelity in a stream dwelling cyprinid, *Leuciscus leuciscus*. *Journal of Fish Biology*, 50, 1117–1119.
- COLLARES-PEREIRA, M.J. AND COWX, I.G., 2004. The role of catchment scale environmental management in freshwater fish conservation. *Fisheries Management and Ecology*, 11, 303–312.
- COLLARES-PEREIRA, M.J., COWX, I.G. AND COELHO, M.M., eds., 2002. *Conservation of freshwater fish: options for the future*. Oxford: Fishing News Books, Blackwell Science.
- CONNELL, J.H. AND KEOUGH, M.J., 1985. Disturbance and patch dynamics of subtidal marine animals on hard substrata. In: PICKETT, S.T.A. AND WHITE, P.S., eds. *The ecology of natural disturbance and patch dynamics*. New York: Academic Press, 125–151.
- CONNELL, J.H. AND SOUSA, W.P., 1983. On the evidence needed to judge ecological stability or persistence. *American Naturalist*, 121, 789–824.
- CONNELL, J.H., 1978. Diversity in tropical rain forests and coral reefs. *Science*, 199, 1302–1310.
- COPP, G.H. AND MANN, R.H.K., 1993. Comparative growth and diet of tench *Tinca tinca* (L.) larvae and juveniles from river floodplain biotopes in France and England. *Ecology of Freshwater Fish*, 2, 58–66.
- COPP, G.H., 1993. Microhabitat use of fish larvae and 0+ juveniles in a small abandoned channel of the upper River Rhone, France. *Folia Zoologica*, 42, 153–164.

- COPP, G.H. AND PEŇÁZ, M., 1988. Ecology of fish spawning and nursery zones in the floodplain, using a new sampling approach. *Hydrobiologia*, 169, 209–224.
- COPP, G.H., 1989. The habitat diversity and fish reproduction function of floodplain ecosystems. *Environmental Biology of Fishes*, 26, 1–27.
- COPP, G.H., 1990. Recognition of cohorts and growth of larval and juvenile roach *Rutilus rutilus* (L.), using size-class ordination of developmental steps. *Journal of Fish Biology*, 36, 803–819.
- COPP, G.H., 1992. Comparative microhabitat use of cyprinid larvae and juveniles in a lotic flood plain channel. *Environmental Biology of Fishes*, 33, 181–193.
- COPP, G.H., 1997a. Microhabitat use of fish larvae and 0(+) juveniles in a highly regulated section of the River Great Ouse. *Regulated Rivers: Research and Management*, 13, 267–276.
- COPP, G.H., 1997b. Importance of marinas and off channel water bodies as refuges for young fishes in a regulated lowland river. *Regulated Rivers: Research and Management*, 13, 303–307.
- COPP, G.H., GUTI, G., ROVNÝ, B. AND ČERNÝ, J., 1994. Hierarchical analysis of habitat use by 0+ juvenile fish in Hungarian/Slovak flood plain of the Danube River. *Environmental Biology of Fishes*, 40, 329–348.
- COPP, G.H., OLIVIER, J.M., PEŇÁZ, M. AND ROUX, A.L., 1991. Juvenile fishes as functional describers of fluvial ecosystem dynamics: applications on the River Rhône, France. *Regulated Rivers: Research and Management*, 6, 135–145.
- COSTELLO, M.J., 1990. Predator feeding strategy and prey importance: a new graphical analysis. *Journal of Fish Biology*, 36, 261–263.
- COTE, D., SCRUTON, D.A., COLE, L. AND MCKINLEY, R.S., 1999. Swimming performance and growth rates of juvenile Atlantic cod intraperitoneally implanted with dummy acoustic transmitters. *North American Journal of Fisheries Management*, 19, 1137–1141.
- COWX, I.G., FISHER, K.A.M. AND BROUGHTON, N.M., 1986. The use of anglers' catches to monitor fish populations in large water bodies, with particular reference to the River Derwent, Derbyshire, England. *Aquaculture and Fisheries Management*, 17, 95–103.
- COWX, I.G. AND GERDEAUX, D., 2004. The effects of fisheries management practises on freshwater ecosystems. *Fisheries Management and Ecology*, 11, 145–152.
- COWX, I.G. AND VAN ZYLL DE JONG, M., 2004. Rehabilitation of freshwater fisheries: tales of the unexpected? *Fisheries Management and Ecology*, 11, 243–249.
- COWX, I.G. AND WELCOMME, R.L., eds., 1998. *Rehabilitation of rivers for fish*. Oxford: Fishing News Books, Blackwell Science.
- COWX, I.G., ed., 1998. *Stocking and introduction of fish*. Oxford: Fishing News Books, Blackwell Science.
- COWX, I.G., 1994. Stocking strategies. *Fisheries Management and Ecology*, 1, 15–30.
- COWX, I.G., 1999. An appraisal of stocking strategies in the light of developing country constraints. *Fisheries Management and Ecology*, 6, 21–34.
- COWX, I.G., 2002. Analysis of threats to freshwater fish conservation: past and present challenges. In: COLLARES-PEREIRA, M.J., COWX, I.G. AND COELHO, M.M., eds. *Conservation of freshwater fish: options for the future*. Oxford: Fishing News Books, Blackwell Science, 201–220.
- COWX, I.G., NOBLE, R.A.A., NUNN, A.D., HARVEY, J.P., WELCOMME, R.L. AND HALLS, A., 2004. *Flow and level criteria for coarse fish and conservation species*. Bristol: Environment Agency, (Science Report SC020112/SR).
- COWX, I.G., NUNN, A.D. AND HARVEY, J.P., 2001. Quantitative sampling of 0-group fish populations in large lowland rivers: point abundance sampling by electric fishing versus micromesh seine netting. *Archiv für Hydrobiologie*, 151: 369–382.
- CRAIG, J.F., HALLS, A.S., BARR, J.J.F. AND BEAN, C.W., 2004. The Bangladesh floodplain fisheries. *Fisheries Research*, 66, 271–286.

- CRISP, D.T. AND HURLEY, M.A., 1991. Stream channel experiments on downstream movement of recently emerged trout, *Salmo trutta* L. and salmon, *S. salar* L. –I. Effect of four different water velocity treatments upon dispersal rate. *Journal of Fish Biology*, 39, 347–361.
- CROOK, D.A., 2004. Is the home range concept compatible with the movements of two species of lowland river fish? *Journal of Animal Ecology*, 73, 353–366.
- CUNJAK, R.A., AND POWER, G., 1986. Winter habitat utilization by stream resident brook trout (*Salvelinus fontinalis*) and brown trout (*Salmo trutta*). *Canadian Journal of Fisheries and Aquatic Sciences*, 43, 1970–1981.
- DAS MAHAPATRA, K., GJERDE, B., REDDY, P.V.G.K., SAHOO, M., JANA, R.K., SAHA, J.N. AND RYE, M., 2001. Tagging: on the use of passive integrated transponder (PIT) tags for the identification of fish. *Aquaculture Research*, 32, 47–50.
- DAVID, B.O. AND CLOSS, G.P., 2002. Behavior of a stream-dwelling fish before, during, and after high-discharge events. *Transactions of the American Fisheries Society*, 131, 762–771.
- DEANGELIS, D.L., LOFTUS, W.F., TREXLER, J.C. AND ULANOWICZ, R.E., 1997. Modelling fish dynamics and effects of stress in a hydrologically pulsed ecosystem. *Journal of Aquatic Ecosystem Stress and Recovery*, 6, 1–13.
- DEEGAN, L.A., GOLDEN, H., HARVEY, C.J. AND PETERSON, B.J., 1999. Influence of environmental variability on the growth of age-0 and adult arctic grayling. *Transactions of the American Fisheries Society*, 128, 1163–1175.
- DEFRA, 2005. *Making space for water – towards a new government strategy for flood and coastal erosion risk management in England*. London: DEFRA Publications.
- DETTMERS, J.M., WAHL, D.H., SOLUK, D.A. AND GUTREUTER, S., 2001. Life in the fast lane: fish and food web structure in the main channel of large rivers. *Journal of the North American Benthological Society*, 20, 255–265.
- DEVRIES, P., 1997. Riverine salmonid egg burial depths: review of published data and implications for scour studies. *Canadian Journal of Fisheries and Aquatic Sciences*, 54, 1685–1698
- DEWEY, M.R. AND ZIGLER, S.J., 1996. An evaluation of fluorescent elastomer for marking bluegill sunfish in experimental studies. *The Progressive Fish Culturist*, 58, 219–220.
- DOLLOFF, C.A., FLEBBE, P.A. AND OWEN, M.D., 1994. Fish habitat structure and fish populations in a southern Appalachian watershed before and after Hurricane Hugo. *Transactions of the American Fisheries Society*, 123, 668–678.
- DOUPE, R.G., PARTRIDGE, G.J. AND LYMBERY, A.J., 2003. Visible implant fluorescent elastomer tags as pedigree markers for applied aquaculture: an evaluation using black bream *Acanthopagrus butcheri*. *Aquaculture Research*, 34, 681–683.
- DUDGEON, D., 2000. Riverine wetlands and biodiversity conservation in tropical Asia. In: GOPAL, B., JUNK, W.J. AND DAVIS, J.A., eds. *Biodiversity in wetlands: assessment, function and conservation*. Leiden, the Netherlands: Backhuys Publishers, 35–60.
- DUSSAULT, C. AND RODRIGUEZ, M.A., 1997. Field trials of marking stream salmonids by dye injection and coded-wire-tagging. *North American Journal of Fisheries Management*, 17, 451–456.
- DYNESIUS, M. AND NILSSON, C., 1994. Fragmentation and flow regulation of river systems in the northern third of the world. *Science*, 266, 753–762.
- ELWOOD, J.W. AND WATERS, T.F., 1969. Effects of floods on food consumption and production rates of a stream brook trout population. *Transactions of the American Fisheries Society*, 98, 253–262.
- ERMAN, D.C., ANDREWS, E.D. AND YODER-WILLIAMS, M., 1988. Effects of winter floods on fishes in the Sierra Nevada. *Canadian Journal of Fisheries and Aquatic Sciences*, 45, 2195–2200.

- FACEY, D.E. AND GROSSMAN, G.D., 1990. The metabolic cost of maintaining position for four North American stream fishes: effects of season and velocity. *Physiological Zoology*, 63, 757–776.
- FAROOQI, M.A. AND MORGAN, C.E., 1996. Elastomer visible implant (EVI) tag retention and the effect of tagging on the growth and survival of barbel, *Barbus barbus* (L.). *Fisheries Management and Ecology*, 3, 181–183.
- FAUSCH, K.D. AND BRAMBLETT, R.G., 1991. Disturbance and fish communities in intermittent tributaries of a western Great Plains river. *Copeia*, 1991, 659–674.
- FAUSCH, K.D., TANIGUCHI, Y., NAKANO, S., GROSSMAN, G.D. AND TOWNSEND, C.R., 2001. Flood disturbance regimes influence rainbow trout invasion success among five holarctic regions. *Ecological Applications*, 11, 1438–1455.
- FERNANDES, C.C., 1997. Lateral migration of fishes in Amazon floodplains. *Ecology of Freshwater Fish*, 6, 36–44.
- FEYRER, F., SOMMER, T.R., ZEUG, S.C., O'LEARY, G. AND HARRELL, W., 2004. Fish assemblages of perennial floodplain ponds of the Sacramento River, California (USA), with implications for the conservation of native fishes. *Fisheries Management and Ecology*, 11, 335–344.
- FISH, F.E. AND LAUDER, G.V., 2006. Passive and active flow control by swimming fishes and mammals. *Annual Review of Fluid Mechanics*, 38, 193–224.
- FITZGERALD, J.L., SHEEHAN, T.F. AND KOCIK, J.F., 2004. Visibility of visual implant elastomer tags in Atlantic salmon reared for two years in marine net-pens. *North American Journal of Fisheries Management*, 24, 222–227.
- FONTENOT, Q.C., RUTHERFORD, D.A. AND KELSO, W.E., 2001. Effects of environmental hypoxia associated with the annual flood pulse on the distribution of larval sunfish and shad in the Atchafalaya River Basin, Louisiana. *Transactions of the American Fisheries Society*, 130, 107–116.
- FRANSSSEN, N.R., GIDO, K.B., GUY, C.S., TRIPE, J.A., SHRANK, S.J., STRAKOSH, T.R., BERTRAND, K.N., FRANSSSEN, C.M., PITTS, K.L. AND PAUKERT, C.P., 2006. Effects of floods on fish assemblages in an intermittent prairie stream. *Freshwater Biology*, 51, 2072–2086.
- FRASER, D.F., GILLIAM, J.F., ALBANESE, B.W. AND SNIDER, S.B., 2006. Effects of temporal patterning of predation threat on movement of a stream fish: evaluating an intermediate threat hypothesis. *Environmental Biology of Fish*, 76, 25–35.
- FREDERICK, J.L., 1997. Evaluation of fluorescent elastomer injection as a method for marking small fish. *Bulletin of Marine Science*, 61, 399–408.
- FREDRICH, F., OHMANN, S., CURIO, B. AND KIRSCHBAUM, F., 2003. Spawning migrations of the chub in the River Spree, Germany. *Journal of Fish Biology*, 63, 710–723.
- FREEMAN, M.C., 1995. Movements by two small fishes in a large stream. *Copeia*, 1995, 361–367.
- GALAT, D.L., FREDRICKSON, L.H., HUMBURG, D.D., BATAILLE, K.J., BODIE, J.R., DOHRENWEND, J., GELWICKS, G.T., HAVEL, J.E., HELMERS, D.L., HOOKER, J.B., JONES, J.R., KNOWLTON, M.F., KUBISIAK, J., MAZOUREK, J., MCCOLPIN, A.C., RENKEN, R.B. AND SEMLITSCH, R.D., 1998. Flooding to restore connectivity of regulated, large-river wetlands. *Bioscience*, 48, 721–733.
- GARNER, P., 1996. Microhabitat use and diet of 0+ cyprinid fishes in a lentic, regulated reach of the River Great Ouse, England. *Journal of Fish Biology*, 48, 367–382.
- GARNER, P., 1997a. Habitat use by 0+ cyprinid fish in the River Great Ouse, East Anglia. *Freshwater Forum*, 8, 2–27.
- GARNER, P., 1997b. Seasonal variation in the habitat available for 0+ *Rutilus rutilus* (L.) in a regulated river. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 7, 199–210.
- GAUDREAU, N. AND BOISCLAIR, D., 2000. Influence of moon phase on acoustic estimates of fish performing daily horizontal migration in a small oligotrophic lake. *Canadian Journal of Aquatic Sciences*, 57, 581–590.

- GEHRKE, P.C., 1990. Spatial and temporal dispersion patterns of golden perch, *Macquaria ambigua*, larvae in an artificial floodplain environment. *Journal of Fish Biology*, 37, 225–236.
- GEHRKE, P.C., 1992. Diel abundance, migration and feeding of fish larvae (eleotridae) in a floodplain billabong. *Journal of Fish Biology*, 40, 695–707.
- GEHRKE, P.C., ASTLES, K.L. AND HARRIS, J.H., 1999. Within-catchment effects of flow alteration on fish assemblages in the Hawkesbury-Nepean river system, Australia. *Regulated Rivers: Research and Management*, 15, 181–198.
- GEHRKE, P.C., BROWN, P., SCHILLER, C.B., MOFFATT, D.B. AND BRUCE, A.M., 1995. River regulation and fish communities in the Murray-Darling River system, Australia. *Regulated Rivers: Research and Management*, 11, 363–375.
- GEHRKE, P.C., REVELL, M.B. AND PHILBEY, A.W., 1993. Effects of river red gum, *Eucalyptus camaldulensis*, litter on golden perch, *Macquaria ambigua*. *Journal of Fish Biology*, 43, 265–79.
- GERKING, S.D., 1953. Evidence for the concepts of home range and territory in stream fishes. *Ecology*, 34, 347–365.
- GERSTNER, C.L., 2007. Effect of oral suction and other friction-enhancing behaviors on the station-holding performance of suckermouth catfish (*Hypostomus spp.*). *Canadian Journal of Zoology-Revue Canadienne de Zoologie*, 85, 133–140.
- GIBBONS, J.W. AND ANDREWS, K.M., 2004. PIT tagging: simple technology at its best. *Bioscience*, 54, 447–454.
- GIBSON, C.A., MEYER, J.L., POFF, N.L., HAY, L.E. AND GEORGAKAKOS, A., 2005. Flow regime alterations under changing climate in two river basins: Implications for freshwater ecosystems. *River Research and Applications*, 21, 849–864.
- GILLETTE, D.P., TIEMANN, J.S., EDDS, D.R. AND WILDHABER, M.L., 2006. Habitat use by a Midwestern U.S.A. riverine fish assemblage: effects of season, water temperature and river discharge. *Journal of Fish Biology*, 68, 1494–1512.
- GILLIAM, J.F. AND FRASER, D.F., 2001. Movement in corridors: enhancement by predation threat, disturbance, and habitat structure. *Ecology*, 82, 258–273.
- GITAY, H, SUÁREZ, A, WATSON, R.T. AND DOKKEN, D.J., eds., 2002. *Climate change and biodiversity*. Geneva, Switzerland: Intergovernmental Panel on Climate Change.
- GLIWICZ, Z.M. AND JACHNER, A., 1992. Diel migrations of juvenile fish: a ghost of predation past or present? *Archiv für Hydrobiologie*, 124, 385–410.
- GLIWICZ, Z.M., SLON, J. AND SZYNKARCZYK, I., 2006. Trading safety for food: evidence from gut contents in roach and bleak captured at different distances offshore from their daytime littoral refuge. *Freshwater Biology*, 51, 823–839.
- GOLDSMITH, R.J., CLOSS, G.P. AND STEEN, H., 2003. Evaluation of visible implant elastomer for individual marking of small perch and common bully. *Journal of Fish Biology*, 63, 631–636.
- GOMES, L.C. AND AGOSTINHO, A.A., 1997. Influence of the flooding regime on the nutritional state and juvenile recruitment of the curimba, *Prochilodus scrofa*, Steindachner, in Upper Parana, Brazil. *Fisheries Management and Ecology*, 4, 263–274.
- GORE, J.A. AND SHIELDS, Jr., F.D., 1995. Can large rivers be restored? A focus on rehabilitation. *Bioscience*, 45, 142–152.
- GOWAN, C. AND FAUSCH, K.D., 2002. Why do foraging stream salmonids move during summer? *Environmental Biology of Fishes*, 64, 139–153.
- GOWAN, C., YOUNG, M.K., FAUSCH, K.D. AND RILEY, S.C., 1994. Restricted movement in resident stream salmonids: a paradigm lost? *Canadian Journal of Fisheries and Aquatic Sciences*, 51, 2626–2637.
- GREMILLET, D., WRIGHT, G., LAUDER, A., CARSS, D.N. AND WANLESS, S., 2003. Modelling the daily food requirements of wintering great cormorants: a bioenergetics tool for wildlife management. *Journal of Applied Ecology*, 40, 266–277.

- GRIES, G. AND LETCHER, B.H., 2002. Tag retention and survival of age-0 Atlantic salmon following surgical implantation with passive integrated transponder tags. *North American Journal of Fisheries Management*, 22, 219–222.
- GRIFT, R.E., BUIJSE, A.D., KLEIN BRETELER, J.G.P., VAN DENSEN, W.L.T., MACHIELS, M.A.M. AND BACKX, J.J.G.M., 2001a. Migration of bream between the main channel and floodplain lakes along the lower River Rhine during the connection phase. *Journal of Fish Biology*, 59, 1033–1055.
- GRIFT, R.E., BUIJSE, A.D., VAN DENSEN, W.L.T. AND KLEIN BRETELER, J.G.P., 2001b. Restoration of the river-floodplain interaction: benefits for the fish community in the River Rhine. *Archiv für Hydrobiologie Supplement*, 135, 173–185.
- GRIFT, R.E., BUIJSE, A.D., VAN DENSEN, W.L.T., MACHIELS, M.A.M., KRANENBARG, J., BRETELER, J.P.K. AND BANKX, J.J.G.M., 2003. Suitable habitats for 0-group fish in rehabilitated floodplains along the lower River Rhine. *River Research and Applications*, 19, 353–374.
- GRIFT, R.E., 2001. *How fish benefit from floodplain restoration along the Lower River Rhine*. Unpublished PhD thesis, Wageningen University.
- GUILLORY, V., 1979. Utilization of an inundated floodplain by Mississippi River fishes. *Florida Scientist*, 42, 222–228.
- GUTREUTER, S., BARTELS, A.D., IRONS, K. AND SANDHEINRICH, M.B., 1999. Evaluation of the flood-pulse concept based on statistical models of growth of selected fishes of the upper Mississippi River system. *Canadian Journal of Fisheries and Aquatic Sciences*, 56, 2282–2291.
- GUY, C.S., SCHULTZ, R.D. AND CLOUSE, C.P., 1996. Coded wire tag loss from paddlefish: a function of study location. *North American Journal of Fisheries Management*, 16, 931–934.
- HAEUBER, R.A. AND MICHENER, W.K., 1998. Policy implications of recent natural and managed floods. *Bioscience*, 48, 765–772.
- HALE, R.S. AND GRAY, J.H., 1998. Retention and detection of coded wire tags and elastomer tags in trout. *North American Journal of Fisheries Management*, 18, 197–201.
- HALYK, L.C. AND BALON, E.K., 1983. Structure and ecological production of the fish taxocene of a small floodplain system. *Canadian Journal of Zoology*, 61, 2446–2464.
- HANSON, P.L. AND WATERS, T.F., 1974. Recovery of standing crop and production rates of a brook trout population in a flood damaged stream. *Transactions of the American Fisheries Society*, 103, 431–439.
- HARCUP, M.F., WILLIAMS, R. AND ELLIS, D.M., 1984. Movements of brown trout, *Salmo trutta* L., in the River Gwyddon, South Wales. *Journal of Fish Biology*, 24, 415–426.
- HARRELL, H.L., 1978. Response of the Devil's River fish community to flooding. *Copeia*, 1978, 60–68.
- HARVEY, B.C., 1987. Susceptibility of young-of-the-year fishes to downstream displacement by flooding. *Transactions of the American Fisheries Society*, 116, 851–855.
- HARVEY, B.C., NAKAMOTO, R.J. AND WHITE, J.L., 1999. Influence of large woody debris and a bankfull flood on movement of adult resident coastal cutthroat trout (*Oncorhynchus clarki*) during fall and winter. *Canadian Journal of Fisheries and Aquatic Sciences*, 56, 2161–2166.
- HAUER, F.R. AND LORANG, M.S., 2004. River regulation, decline of ecological resources, and potential for restoration in a semi-arid lands river in the western USA. *Aquatic Sciences*, 66, 388–401.
- HAUER, F.R., BARRON, J.S., CAMPBELL, D.H., FAUSCH, K.D., HOSTETLER, S.W., LEAVESLEY, G.H., LEAVITT, P.R., MCKNIGHT, D.M. AND STANFORD, J.A., 1997. Assessment of climate change and freshwater ecosystems of the Rocky Mountains, USA and Canada. *Hydrological Processes*, 11, 903–924.

- HEERMANN, L. AND BORCHERDING, J., 2006. Winter short-distance migration of juvenile fish between two floodplain water bodies of the Lower River Rhine. *Ecology of Freshwater Fish*, 15, 161–168.
- HEGGBERGET, T.G., 1988. Timing of spawning of Norwegian Atlantic salmon (*Salmo salar*). *Canadian Journal of Fisheries and Aquatic Sciences*, 45, 845–849.
- HEGGENES, J. AND TRAAEN, T., 1988. Downstream migration and critical water velocities in stream channels for fry of four salmonid species. *Journal of Fish Biology*, 32, 717–727.
- HEGGENES, J., 1988. Effects of short-term flow fluctuations on displacement of, and habitat use by, brown trout in a small stream. *Transactions of the American Fisheries Society*, 117, 336–344.
- HELFMAN, G.S., 1993. Fish behaviour by day, night and twilight. In: PITCHER, T.J., ed. *Behaviour of teleost fishes*. London: Chapman and Hall, 285–306.
- HENDERSON, J.N. AND LETCHER, B.H., 2003. Predation on stocked Atlantic salmon (*Salmo salar*) fry. *Canadian Journal of Fisheries and Aquatic Sciences*, 60, 32–42.
- HENNING, J.A., GRESSWELL, R.E. AND FLEMING, I.A., 2007. Use of seasonal freshwater wetlands by fishes in a temperate river floodplain. *Journal of Fish Biology*, 71, 476–492.
- HILDERBRAND, R.H. AND KERSHNER, J.L., 2000. Movement patterns of stream-resident cutthroat trout in Beaver Creek, Idaho–Utah. *Transactions of the American Fisheries Society*, 129, 1160–1170.
- HILDERBRAND, R.H., WATTS, A.C. AND RANDLE, A.M., 2005. The myths of restoration ecology. *Ecology and Society*, 10, 19–29.
- HILL, J. AND GROSSMAN, G.D., 1987. Home range estimates for three North American stream fishes. *Copeia*, 1987, 376–380.
- HOEINGHAUS, D.J., LAYMAN, C.A., ARRINGTON, D.A. AND WINEMILLER, K.O., 2003. Spatiotemporal variation in fish assemblage structure in tropical floodplain creeks. *Environmental Biology of Fishes*, 67, 379–387.
- HOHAUSOVÁ, E., 2000. Exchange rate and small-scale movements of fish between a river and its backwater. *Archiv für Hydrobiologie*, 147, 485–504.
- HOHAUSOVÁ, E., COPP, G.H. AND JANKOVSKY, P., 2003. Movement of fish between a river and its backwater: diel activity and relation to environmental gradients. *Ecology of Freshwater Fish*, 12, 107–117.
- HOOPES, R.L., 1975. Flooding as the result of Hurricane Agnes, and its effects on a native brook trout population in an infertile headwater stream in central Pennsylvania. *Transactions of the American Fisheries Society*, 104, 96–99.
- HUET, M., 1949. Aperçu des relations entre la pente et les populations piscicoles des eaux courantes. *Schweizerische Zeitschrift für Hydrologie*, 11, 333–351.
- HULME, M., JENKINS, G.J., LU, X., TURNPENNY, J.R., MITCHELL, T.D., JONES, R.G., LOWE, J., MURPHY, J.M., HASSELL, D., BOORMAN, P., MCDONALD, R. AND HILL, S., 2002. *Climate change scenarios for the UK: the UKCIP02 scientific report*. Tyndall Centre for Climate Change Research, School of Environmental Sciences, University of East Anglia, Norwich, UK.
- HUMPHRIES, P., COOK, R.A., RICHARDSON, A.M. AND SERAFINI, L.G., 2006. Creating a disturbance: manipulating slackwaters in a lowland river. *River Research and Applications*, 22, 525–542.
- HUMPHRIES, P., KING, A.J. AND KOEHN, J.D., 1999. Fish, flows and floodplains: Links between freshwater fishes and their environment in the Murray-Darling River system, Australia. *Environmental Biology of Fishes*, 56, 129–151.
- HUNTINGFORD, F.A., 1993. Can cost-benefit analysis explain fish distribution patterns? *Journal of Fish Biology*, 43, 289–308.
- HUNTINGFORD, F.A., 2004. Implications of domestication and rearing conditions for the behaviour of cultivated fish. *Journal of Fish Biology*, 65 (Suppl. A), 122–142.
- HURST, T.P., 2007. Causes and consequences of winter mortality in fishes. *Journal of Fish Biology*, 71, 315–345.

- HYNES, H.B.N., 1950. The food of fresh-water sticklebacks (*Gasterosteus aculeatus* and *Pygosteus pungitius*), with a review of methods used in studies of the food of fishes. *Journal of Animal Ecology*, 19, 36–58.
- JACKSON, D.C., 2004. Fisheries dynamics in the Yazoo River Basin. In: WELCOMME, R. AND PETR, T., eds. *Proceedings of the second international symposium on the management of large rivers for fisheries: Volume II*. Bangkok, Thailand: FAO Regional Office for Asia and the Pacific, 103–115, (RAP Publication 2004/17).
- JENSEN, A.J. AND JOHNSEN, B.O., 1999. The functional relationship between peak spring floods and survival and growth of juvenile Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta*). *Functional Ecology*, 13, 778–785.
- JEPSEN, N. AND BERG, S., 2002. The use of winter refuges by roach tagged with miniature radio transmitters. *Hydrobiologia*, 483, 167–173.
- JEPSEN, N., DAVIS, L.E., SCHRECK, C.B. AND SIDDENS, B., 2001. The physiological response of Chinook salmon smolts to two methods of radio-tagging. *Transactions of the American Fisheries Society*, 130, 495–500.
- JEPSEN, N., KOED, A., THORSTAD, E.B. AND BARAS, E., 2002. Surgical implantation of telemetry transmitters in fish: how much have we learned? *Hydrobiologia*, 483, 239–248.
- JOHN, K.R., 1963. The effect of torrential rains on the reproductive cycle of *Rhinichthys osculus* (girard) in the Chiricahua Mountains, Arizona. *Copeia*, 1963, 286–291.
- JOHN, K.R., 1964. Survival of fish in intermittent streams of the Chiricahua Mountains, Arizona. *Ecology*, 45, 112–119.
- JONSSON, N., NÆSJE, T.F., JONSSON, B., SAKSGÅRD, R. AND SANDLUND, O.T., 1999. The influence of piscivory on life history traits of brown trout. *Journal of Fish Biology*, 55, 1129–1141.
- JOWETT, I.G. AND RICHARDSON, J., 1989. Effects of a severe flood on in-stream habitat and trout populations in seven New Zealand rivers. *New Zealand Journal of Marine and Freshwater Research*, 23, 11–17.
- JOWETT, I.G. AND RICHARDSON, J., 1994. Comparison of habitat use by fish in normal and flooded river conditions. *New Zealand Journal of Marine and Freshwater Research*, 2, 409–416.
- JUANES, F., LETCHER, B.H. AND GRIES, G., 2000. Ecology of stream fish: insights gained from an individual-based approach to juvenile Atlantic salmon. *Ecology of Freshwater Fish*, 9, 65–73.
- JUNGWIRTH, M., 1998. River continuum and fish migration – going beyond the longitudinal river corridor in understanding ecological integrity. In: JUNGWIRTH, M., SCHMUTZ, S. AND WEISS, S., eds. *Fish migration and fish bypasses*. Oxford: Fishing News Books, Blackwell Science, 19–32.
- JUNGWIRTH, M., MUHAR, S. AND SCHMUTZ, S., 2000. Fundamentals of fish ecological integrity and their relation to the extended serial discontinuity concept. *Hydrobiologia*, 422–423, 85–97.
- JUNK, W.J. AND WANTZEN, K.M., 2004. The flood pulse concept: new aspects, approaches AND applications – an update. In: WELCOMME, R. AND PETR, T., eds. *Proceedings of the second international symposium on the management of large rivers for fisheries: Volume II*. Bangkok, Thailand: FAO Regional Office for Asia and the Pacific, 117–140, (RAP Publication 2004/17).
- JUNK, W.J., 1999. The flood pulse concept of large rivers: learning from the tropics. *Archiv für Hydrobiologie Supplement*, 115, 261–280.
- JUNK, W.J., BAYLEY, P.B. AND SPARKS, R.E., 1989. The flood pulse concept in river–floodplain systems. *Canadian Special Publication of Fisheries and Aquatic Sciences*, 106, 110–127.
- JURAJDA, P., ONDRAČKOVÁ, M. AND REICHARD, M., 2004. Managed flooding as a tool for supporting natural fish reproduction in man-made lentic waterbodies. *Fisheries Management and Ecology*, 11, 237–242.

- KATANO, O. AND HAKOYAMA, H., 1997. Spawning behavior of *Hemibarbus barbus* (Cyprinidae). *Copeia*, 1997, 620–622.
- KELLEY, J.L. AND MAGURRAN, A.E., 2003. Learned predator recognition and antipredator response in fishes. *Fish and Fisheries*, 4, 216–226.
- KELLY, W.H., 1967. Marking fish with dyes. *Transactions of the American Fisheries Society*, 96, 163–175.
- KENNEDY, T.B. AND VINYARD, G.L., 1997. Drift ecology of western catostomid larvae with emphasis on Warner suckers, *Catostomus warnerensis* (Teleostei). *Environmental Biology of Fishes*, 49, 187–195.
- KILLGORE, K.J. AND BAKER, J.A., 1996. Patterns of larval fish abundance in a bottomland hardwood wetland. *Wetlands*, 16, 288–295.
- KING, A.J., HUMPHRIES, P. AND LAKE, P.S., 2003. Fish recruitment on floodplains: the roles of patterns of flooding and life history characteristics. *Canadian Journal of Fisheries and Aquatic Sciences*, 60, 773–786.
- KNAEPKENS, G., BRUYNDONCX, L. AND EENS, M., 2004. Assessment of residency and movement of the endangered bullhead in two Flemish rivers. *Ecology of Freshwater Fish*, 13, 317–322.
- KRAMER, D.L. AND CHAPMAN, M.R., 1999. Implications of home range size and relocation for marine reserve function. *Environmental Biology of Fishes*, 55, 65–79.
- KRAMER, D.L., RANGELEY, R.W. AND CHAPMAN, L.J., 1997. Habitat selection: patterns of spatial distribution from behavioural decisions. In: GODIN J.J., ed. *Behavioural ecology of teleost fishes*. Oxford: Oxford University Press, 37–80.
- KWAK, T.J., 1988. Lateral movement and use of floodplain habitat by fishes of the Kankakee River, Illinois. *American Midland Naturalist*, 120, 241–249.
- LA RIVERS, I., 1962. *Fishes and fisheries of Nevada*. Reno, Nevada: University of Nevada Press. (Republished by the Nevada State Fish and Game Commission, 1994.)
- LACROIX, G.L., KNOX, D. AND MCCURDY, P., 2004. Effects of implanted dummy acoustic transmitters on juvenile Atlantic salmon. *Transactions of the American Fisheries Society*, 133, 211–220.
- LADLE, M., 2002. *Review of flow needs for fish and fisheries*. Bristol: Environment Agency, (R&D Technical report W159).
- LAKE, P.S., 2000. Disturbance, patchiness, and diversity in streams. *Journal of the North American Benthological Society*, 19, 573–592.
- LAKE, P.S., BOND, N. AND REICH, P., 2007. Linking ecological theory with stream restoration. *Freshwater Biology*, 52, 597–615.
- LAMBERTI, G.A., GREGORY, S.V., ASHKENAS, L.R., WILDMAN, R.C. AND MOORE, K.M.S., 1991. Stream ecosystem recovery following a catastrophic debris flow. *Canadian Journal of Fisheries and Aquatic Sciences*, 48, 196–208.
- LAPOINTE, M., EATON, B., DRISCOLL, S. AND LATULIPPE, C., 2000. Modelling the probability of salmonid egg pocket scour due to floods *Canadian Journal of Fisheries and Aquatic Sciences*, 57, 1120–1130.
- LARGE, A.R.G. AND PETTS, G.E., 1996. Historical channel-floodplain dynamics along the River Trent: implications for river rehabilitation. *Applied Geography*, 16, 191–209.
- LARGE, A.R.G. AND PRACH, K., 1998. Floodplain ecology of the regulated River Trent: implications for rehabilitation. In: BAILEY, R.G., JOSÉ, P.V. AND SHERWOOD, B.R., eds. *United Kingdom floodplains*. Otley, UK: Westbury Academic and Scientific Publishing, 409–421.
- LETCHER, B.H. AND TERRICK, T.D., 1998. Maturation of male age-0 Atlantic salmon following a massive, localized flood. *Journal of Fish Biology*, 53, 1243–1252.
- LILJA, J., KESKINEN, T., MARJOMÄKI, T.J., VALKEAJÄRVI, P. AND KARJALAINEN, J., 2003. Upstream migration activity of cyprinids and percids in a channel, monitored by a horizontal split-beam echosounder. *Aquatic Living Resources*, 16, 185–190.

- LINFIELD, R.S.J., 1985. An alternative concept to home range theory with respect to populations of cyprinids in major river systems. *Journal of Fish Biology*, 27 (Suppl. A), 187–196.
- LOBÓN-CERVIÁ, J., 1996. Response of a stream fish assemblage to a severe spate in northern Spain. *Transactions of the American Fisheries Society*, 125, 913–919.
- LOJKÁSEK, B., LUSK, S., HALACKA, K., LUSKOVÁ, K. AND DROZD, P., 2005. The impact of the extreme floods in July 1997 on the ichthyocenosis of the Oder Catchment area (Czech Republic). *Hydrobiologia*, 548, 11–22.
- LONZARICH, D.G., LONZARICH, M.R. AND WARREN, M.L. JR, 2000. Effects of riffle length on the short term movement of fishes among stream pools. *Canadian Journal of Fisheries and Aquatic Sciences*, 57, 1508–1514.
- LOWE-MCCONNELL, R.H., 1975. *Fish communities in tropical freshwaters*. London: Longman Press.
- LOWE-MCCONNELL, R.H., 1987. *Ecological studies in tropical fish communities*. London: Longman Press.
- LUCAS, M.C. AND BARAS, E., 2000. Methods for studying spatial behaviour of freshwater fishes in the natural environment. *Fish and Fisheries*, 1, 283–316.
- LUCAS, M.C. AND BARAS, E., 2001. *Migration of freshwater fishes*. Oxford: Blackwell Science.
- LUCAS, M.C., 1989. Effects of implanted dummy transmitters on mortality, growth and tissue reaction in rainbow trout, *Salmo gairdneri* Richardson. *Journal of Fish Biology*, 35, 577–587.
- LUCAS, M.C., 2000. The influence of environmental factors on movements of lowland river fish in the Yorkshire Ouse system. *The Science of the Total Environment*, 251/252, 223–232.
- LUCAS, M.C., MERCER, T., ARMSTRONG, J.D., MCGINTY, S. AND RYCROFT, P., 1999. Use of a flat-bed passive integrated transponder antenna array to study the migration and behaviour of lowland river fishes at a fish pass. *Fisheries Research*, 44, 183–191.
- LUSK, S., HALACKA, K. AND LUSKOVA, V., 1998. The effect of an extreme flood on the fish communities in the upper reaches of the Ticha Orlice river (the Labe drainage area). *Czech Journal of Animal Science*, 43, 531–536.
- LUSK, S., HALAČKA, K. AND LUSKOVÁ, V., 2003. Rehabilitating the floodplain of the lower River Dyje for fish. *River Research and Applications*, 19, 281–288.
- LUSK, S., HALAČKA, K., LUSKOVÁ, V. AND HORÁK, V., 2001. Annual dynamics of the fish stock in a backwater of the River Dyje. *Regulated Rivers: Research and Management*, 17, 571–581.
- LYONS, J. AND LUCAS, M.C., 2002. The combined use of acoustic tracking and echosounding to investigate the movement and distribution of common bream (*Abramis brama*) in the River Trent, England. *Hydrobiologia*, 483, 265–273.
- MACDONALD, D.G., MILLIGAN, C.L., MCFARLAND, W.J., CROKE, S., CURRIE, S., HOOKE, B., ANGUS, R.B., TUFTS, B.L. AND DAVIDSON, K., 1998. Condition and performance of juvenile Atlantic salmon (*Salmo salar*), effects of rearing practices on hatchery fish and comparison with wild fish. *Canadian Journal of Fisheries and Aquatic Sciences*, 55, 1208–1219.
- MAGURRAN, A.E., 1988. *Ecological diversity and its measurement*. Princeton, NJ: Princeton University Press.
- MALONE, J.C., FORRESTER, G.E. AND STEELE, M.A., 1999. Effects of subcutaneous microtags on the growth, survival, and vulnerability to predation of small reef fishes. *Journal of Experimental Marine Biology and Ecology*, 237, 243–253.
- MANN, R.H.K. AND BASS, J.A. B., 1997. The critical water velocities of larval roach (*Rutilus rutilus*) and dace (*Leuciscus leuciscus*) and implications for river management. *Regulated Rivers: Research and Management*, 13, 295–301.

- MARCHETTI, M.P. AND MOYLE, P.B., 2001. Keeping alien fishes at bay: effects of flow regime and habitat structure on fish assemblages in a regulated California stream. *Ecological Applications*, 11, 75–87.
- MARSHALL, S. AND ELLIOTT, M., 1997. A comparison of univariate and multivariate numerical and graphical techniques for determining inter- and intraspecific feeding relationships in estuarine fish. *Journal of Fish Biology*, 51, 526–545.
- MARTINELLI, T.L., HANSEL, H.C. AND SHIVELY, R.S., 1998. Growth and physiological responses to surgical and gastric radio transmitter implantation techniques in subyearling Chinook salmon (*Oncorhynchus tshawytscha*). *Hydrobiologia*, 371/372, 79–87.
- MARTY, G.D. AND SUMMERFELT, R.C., 1986. Pathways and mechanisms for expulsion of surgically implanted dummy transmitters from channel catfish. *Transactions of the American Fisheries Society*, 115, 577–589.
- MATHENEY, M.P. AND RABENI, C.F., 1995. Patterns of movement and habitat use by hog suckers in an Ozark stream. *Transactions of the American Fisheries Society*, 124, 886–897.
- MATTHEWS, W.J., 1986. Fish community structure in a temperate stream: stability, persistence, and a catastrophic flood. *Copeia*, 1986, 388–397.
- MATTHEWS, W.J., HARVEY, B.C. AND POWER, M.E., 1994. Spatial and temporal patterns in the fish assemblages of individual pools in a midwestern stream (USA). *Environmental Biology of Fishes*, 39, 381–397.
- MATTHEWS, W.J., SCHORR, M.S. AND MEADOR, M.R., 1996. Effects of experimentally enhanced flows on fishes of a small Texas (USA) stream: Assessing the impact of interbasin transfer. *Freshwater Biology*, 35, 349–362.
- MCDOWALL, R.M., 1976. The role of estuaries in the life cycles of fishes in New Zealand. *Proceedings of the New Zealand Ecological Society*, 23, 27–32.
- MCFARLANE, G.A., WYDOSKI, R.S. AND PRINCE, E.D., 1990. Historical review of the development of external tags and marks. *American Fisheries Society Symposium*, 7, 9–29.
- MCCMAHON, T.E. AND HARTMAN, G.F., 1989. Influence of cover complexity and current velocity on winter habitat use by juvenile coho salmon (*Oncorhynchus kisutch*). *Canadian Journal of Fisheries and Aquatic Sciences*, 46, 1551–1557.
- MEFFE, G.K. AND MINCKLEY, W.L., 1987. Persistence and stability of fish and invertebrate assemblages in a repeatedly disturbed Sonoran Desert stream. *American Midland Naturalist*, 117, 177–191.
- MEFFE, G.K., 1984. Effects of abiotic disturbance on coexistence of predator-prey fish species. *Ecology*, 65, 1525–1534.
- MERTES, L.A.K., 1997. Documentation and significance of the perirheic zone on inundated floodplains. *Water Resources Research*, 33, 1749–1762.
- MILHOUSE, R.T., 1998. Modelling of instream flow needs: the link between sediment and aquatic habitat. *Regulated Rivers: Research and Management*, 13, 79–94.
- MILLER, R.R., 1946. *Gila cypha*, a remarkable new species of cyprinid fishes from the Colorado River in Grand Canyon, Arizona. *Journal of Washington Academy of Sciences*, 36, 409–415.
- MION, J.B., STEIN, R.A. AND MARSCHALL, E.A., 1998. River discharge drives survival of larval walleye. *Ecological Applications*, 8, 88–103.
- MODDE, T., BURNHAM, K.P. AND WICK, E.F., 1996. Population status of the endangered razorback sucker in the middle Green River. *Conservation Biology*, 10, 110–119.
- MODDE, T., MUTH, R.T. AND HAINES, G.B., 2001. Floodplain wetland suitability, access, and potential use by juvenile razorback suckers in the middle Green River, Utah. *Transactions of the American Fisheries Society*, 130, 1095–1105.
- MOLLES, M.C., CRAWFORD, C.S., ELLIS, L.M., VALETT, H.M. AND DAHM, C.N., 1998. Managed flooding for riparian ecosystem restoration. *Bioscience*, 48, 749–756.

- MOLLS, F. AND NEUMANN, D., 1994. Fish abundance and fish migration in gravel-pit lakes connected with the River Rhine. *Water Sciences and Technology*, 29, 307–309.
- MOLLS, F., 1999. New insights into the migration and habitat use by bream and white bream in the floodplain of the River Rhine. *Journal of Fish Biology*, 55, 1187–1200.
- MONTGOMERY, D.R., BEAMER, E.M., PESS, G.R. AND QUINN, T.P., 1999. Channel type and salmonid spawning distribution and abundance. *Canadian Journal of Fisheries and Aquatic Sciences*, 56, 377–387
- MONTGOMERY, D.R., BUFFINGTON, J.M., PETERSON, N.P., SCHUETTHAMES, D. AND QUINN, T.P., 1996. Stream-bed scour, egg burial depths, and the influence of salmonid spawning on bed surface mobility and embryo survival. *Canadian Journal of Fisheries and Aquatic Sciences*, 53, 1061–1070.
- MOORE, A., RUSSELL, I.C. AND POTTER, E.C.E., 1990. The effects of intraperitoneally implanted dummy acoustic transmitters on the behaviour and physiology of juvenile Atlantic salmon. *Journal of Fish Biology*, 37, 713–721.
- MOORE, K.M.S. AND GREGORY, S.V., 1988. Response of young-of-the-year cutthroat trout to manipulations of habitat structure in a small stream. *Transactions of the American Fisheries Society*, 117, 162–170.
- MOURSUND, R.A., CARLSON, T.J. AND PETERS, R.D., 2003. A fisheries application of a dual-frequency identification sonar acoustic camera. *ICES Journal of Marine Science*, 60, 678–683.
- MOYLE, P.B. AND LIGHT, T., 1996a. Biological invasions of freshwater: Empirical rules and assembly theory. *Biological Conservation*, 78, 149–161.
- MOYLE, P.B. AND LIGHT, T., 1996b. Fish invasions in California: Do abiotic factors determine success? *Ecology*, 77, 1666–1670.
- NAESJE, T., JONSSON, B. AND SKURDAL, J., 1995. Spring flood: a primary cue for hatching of river spawning Coregoninae. *Canadian Journal of Fisheries and Aquatic Sciences*, 52, 2190–2196
- NAIMAN, R.J. AND DÉCAMPS, H., 1997. The ecology of interfaces: Riparian zones. *Annual Review Ecology and Systematics*, 28, 621–658.
- NAKAMURA, T., MARUYAMA, T. AND WATANABE, S., 2002. Residency and movement of stream-dwelling Japanese charr, *Salvelinus leucomaenis*, in a central Japanese mountain stream. *Ecology of Freshwater Fish*, 11, 150–157.
- NATSUMEDA, T., 2003. Effects of a severe flood on the movements of Japanese fluvial sculpin. *Environmental Biology of Fishes*, 68, 417–424.
- NEAL, C. AND ROBSON, A.J., 2000. A summary of river water quality data collected within the Land-Ocean Interaction Study: core data for eastern UK rivers draining to the North Sea. *The Science of the Total Environment*, 251/252, 585–665.
- NEHRING, R.B. AND ANDERSON, R.M., 1993. Determination of population-limiting critical salmonid habitats in Colorado streams using the Physical Habitat Simulation System. *Rivers*, 4, 1–19.
- NESLER, T.P., MUTH, R.T. AND WASOWICZ, A.F., 1988. Evidence for baseline flow spikes as spawning cues for Colorado squawfish in the Yampa River, Colorado. *Transactions of the American Fisheries Society Symposium*, 5, 68–79.
- NEUMANN, D., SEIDENBERG-BUSSE, C., PETERMEIER, A., STAAS, S., MOLLS, F. AND RUTSCHKE, J., 1994. Gravel-pit lakes connected with the River Rhine as a reserve for high productivity of plankton and young fish. *Water Science and Technology*, 29, 267–271.
- NEUMANN, D., STAAS, S., SEIDENBERG-BUSSE, C., PETERMAIER, A. AND RUTSCHKE, J., 1996. The significance of man-made lentic waters to the ecology of the Lower River Rhine, especially for the recruitment of potamal fish. *Archiv für Hydrobiologie Supplement*, 113, 267–278.
- NICKELSON, T.E., ROGERS, J.D., JOHNSON, S.L. AND SOLAZZI, M.F., 1992. Seasonal changes in habitat use by juvenile coho salmon (*Oncorhynchus kisutch*)

- in Oregon coastal streams. *Canadian Journal of Fisheries and Aquatic Sciences*, 49, 783–789.
- NIENHUIS, P.H. AND LEUVEN, R.S.E.W., 2001. River restoration and flood protection: controversy or synergism? *Hydrobiologia*, 444, 85–99.
- NILSSON, C., REIDY, C.A., DYNESIUS, M. AND REVENGA, C., 2005. Fragmentation and flow regulation of the world's large river systems. *Science*, 308, 405–408.
- NUNN, A.D., HARVEY, J.P. AND COWX, I.G., 2007a. Benefits to 0+ fishes of connecting man-made waterbodies to the lower River Trent, England. *River Research and Applications*, 23, 361–376.
- NUNN, A.D., HARVEY, J.P., BRITTON, J.R., FREAR, P.A. AND COWX, I.G., 2007b. Fish, climate and the Gulf Stream: the influence of abiotic factors on the recruitment success of cyprinid fishes in lowland rivers. *Freshwater Biology*, 52, 1576–1586.
- ODLING-SMEE, L. AND BRAITHWAITE, V.A., 2003. The influence of habitat stability on landmark use during spatial learning in the three-spined stickleback. *Animal Behaviour*, 65, 701–707.
- OLLA, B.L. AND DAVIS, M.W., 1989. The role of learning and stress in predator avoidance of hatchery-reared coho salmon (*Oncorhynchus kisutch*) juveniles. *Aquaculture*, 76: 209–214.
- OLSEN, E.M. AND VØLLESTAD, L.A., 2001. An evaluation of visible implant elastomer for marking age-0 brown trout. *North American Journal of Fisheries Management*, 21, 967–970.
- OMBREDANE, D., BAGLINIERE, J.L. AND MARCHAND, F., 1998. The effects of Passive Integrated Transponder tags on survival and growth of juvenile brown trout (*Salmo trutta* L.) and their use for studying movement in a small river. *Hydrobiologia*, 371/372, 99–106.
- ORTLEPP, J. AND MURLE, U., 2003. Effects of experimental flooding on brown trout (*Salmo trutta fario* L.): The River Spol, Swiss National Park. *Aquatic Sciences*, 65, 232–238.
- OTTAWAY, E.M. AND FORREST, D.R., 1983. The influence of water velocity on the downstream movement of alevins and fry of brown trout, *Salmo trutta* L. *Journal of Fish Biology*, 23, 221–227.
- PAUKERT, C.P., CHVALA, P.J., HEIKES, B.L. AND BROWN, M.L., 2001. Effects of implanted transmitter size and surgery on survival, growth, and wound healing of bluegill. *Transactions of the American Fisheries Society*, 130, 975–980.
- PEARSONS, T.N., LI, H.W. AND LAMBERTI, G.A., 1992. Influence of habitat complexity on resistance to flooding and resilience of stream fish assemblages. *Transactions of the American Fisheries Society*, 121, 427–436.
- PEŇÁZ, M., 2001. A general framework of fish ontogeny: a review of the ongoing debate. *Folia Zoologica*, 50, 241–256.
- PEŇÁZ, M., ROUX, A.-L., JURAJDA, P. AND OLIVIER, J.-M., 1992. Drift of larval and juvenile fishes in by-passed floodplain in the upper River Rhone, France. *Folia Zoologica*, 41, 281–288.
- PENCZAK, T., 2006. Movement pattern and growth ratio of tagged fish in two lowland rivers of central Poland. *Polish Journal of Ecology*, 54, 267–282.
- PERRY, R.W., ADAMS, N.S. AND RONDORF, D.W., 2001. Buoyancy compensation of juvenile Chinook salmon implanted with two different size dummy transmitters. *Transactions of the American Fisheries Society*, 130, 46–52.
- PETERSON, J.T. AND KWAK, T.J., 1999. Modeling the effects of land use and climate change on riverine smallmouth bass. *Ecological Applications*, 9, 1391–1404.
- PETERSON, N.P., PRENTICE, E.F. AND QUINN, T.P., 1994. Comparison of sequential coded wire and passive integrated transponder tags for assessing overwinter growth and survival of juvenile coho salmon. *North American Journal of Fisheries Management*, 14, 870–873.

- PETRY, A.C., AGOSTINHO, A.A. AND GOMES, L.C., 2003a. Fish assemblages of tropical floodplain lagoons: exploring the role of connectivity in a dry year. *Neotropical Ichthyology*, 1, 111–119.
- PETRY, A.C., AGOSTINHO, A.A. AND GOMES, L.C., 2003b. Spatial variation of the fish assemblage structure from the upper Rio Paraná floodplain, Brazil, in a dry year. *Acta Limnologica*, 15, 1–13.
- PETRY, P., BAYLEY, P.B. AND MARKLE, D.F., 2003c. Relationships between fish assemblages, macrophytes and environmental gradients in the Amazon River floodplain. *Journal of Fish Biology*, 63, 547–579.
- PETTS, G.E., MOLLER, H. AND ROUX A.L., eds., 1989. *Historical change of large alluvial rivers: Western Europe*. Chichester, UK: Wiley.
- PHILLIPS, R.W., LANTZ, R.L., CLAIRE, E.W. AND MORING, J.R., 1975. Some effects of gravel mixtures on emergence of coho salmon and steelhead trout fry. *Transactions of the American Fisheries Society*, 104, 461–466.
- PINDER, A.C., 2001. *Keys to larval and juvenile stages of coarse fishes from fresh waters in the British Isles*. Ambleside, UK: Freshwater Biological Association, (Scientific Publication No. 60).
- PINDER, L.C.V., 1997. Research on the Great Ouse: Overview and implications for management. *Regulated Rivers: Research and Management*. 13, 309–315.
- PINDER, L.C.V., MARKER, A.F.H., MANN, R.H.K., BASS, J.A.B. AND COPP, G.H., 1997. The River Great Ouse, a highly eutrophic, slow-flowing, regulated, lowland river in eastern England. *Regulated Rivers: Research and Management*. 13, 203–218.
- PIRES, A.M., MAGALHÃES, M.F., MOREIRA DA COSTA, L., ALVES, M.J. AND COELHO M.M., 2008. Effects of an extreme flash flood on the native fish assemblages across a Mediterranean catchment. *Fisheries Management and Ecology*, 15, 49–58.
- PITCHER, T.J. AND PARRISH, J.K., 1993. Functions of shoaling behaviour in teleosts. *In: PITCHER, T.J., ed. Behaviour of teleost fishes*. London: Chapman and Hall, 363–439.
- POFF, N.L. AND ALLAN, J.D., 1995. Functional organization of stream fish assemblages in relation to hydrological variability. *Ecology*, 76, 606–627.
- POFF, N.L., 1992. Why disturbances can be predictable: a perspective on the definition of disturbance in streams. *Journal of the North American Benthological Society*, 11, 86–92.
- POFF, N.L., 1997. Landscape filters and species traits: towards mechanistic understanding and prediction in stream ecology. *Journal of the North American Benthological Society*, 16, 391–409.
- POFF, N.L., 2002. Ecological response to and management of increased flooding due to climate change. *Proceedings of the Royal Society of London (A)*, 360, 1497–1510.
- POFF, N.L., ALLAN, J.D., BAIN, M.B., KARR, J.R., PRESTEGAARD, K.L., RICHTER, B.D., SPARKS, R.E. AND STROMBERG, J.C., 1997. The natural flow regime. *Bioscience*, 47, 769–784.
- POFF, N.L., OLDEN, J.D., PEPIN, D.M. AND BLEDSOW, B.P., 2006. Placing global stream flow variability in geographic and geomorphic contexts. *River Research and Applications*, 22, 149–166.
- POIZAT, G. AND CRIVELLI, A.J., 1997. Use of seasonally flooded marshes by fish in a Mediterranean wetland: timing and demographic consequences. *Journal of Fish Biology*, 51, 106–119.
- PORTZ, D.E. AND TYUS, H.M., 2004. Fish humps in two Colorado River fishes: a morphological response to cyprinid predation? *Environmental Biology of Fishes*, 71, 233–245.
- POUILLY, M. AND RODRIGUEZ, M.A., 2004. Determinism of fish assemblage structure in neotropical floodplain lakes: influence of internal and landscape lake conditions. *In: WELCOMME, R. AND PETR, T., eds. Proceedings of the second*

- international symposium on the management of large rivers for fisheries: Volume II*. Bangkok, Thailand: FAO Regional Office for Asia and the Pacific, 243–265, (RAP Publication 2004/17).
- POWER, M.E., DIETRICH, W.E. AND FINLAY, J.C., 1996. Dams and downstream aquatic biodiversity: Potential food web consequences of hydrologic and geomorphic change. *Environmental Management*, 20, 887–95.
- PRENTICE, E.F., FLAGG, T.A. AND MCCUTCHEON, C.S., 1990a. Feasibility of using implantable passive integrated transponder PIT tags in salmonids. *American Fisheries Society Symposium*, 7, 317–322.
- PRENTICE, E.F., FLAGG, T.A., MCCUTCHEON, C.S. AND BRASTOW, D.F., 1990b. PIT-tag monitoring systems for hydroelectric dams and fisheries. *American Fisheries Society Symposium*, 7, 323–334.
- PUCKRIDGE, J.T., SHELDON, F., WALKER, K.F. AND BOULTON, A.J., 1998. Flow variability and the ecology of large rivers. *Marine and Freshwater Research*, 49, 55–72.
- RAAT, A.J.P., 2001. Ecological rehabilitation of the Dutch part of the River Rhine with special attention to the fish. *Regulated Rivers: Research and Management*, 17, 131–144.
- RAKOWITZ, G. AND ZWEIMULLER, I., 2000. Influence of diurnal behaviour rhythms and water level fluctuations on the migratory activities of fish in a backwater of the River Danube: a hydroacoustic study. *Aquatic Living Resources*, 13, 319–326.
- REEVES, G.H., BENDA, L.E., BURNETT, K.M., BISSON, P.A. AND SEDELL, J.R., 1995. A disturbance-based ecosystem approach to maintaining and restoring freshwater habitats of evolutionary significant units of anadromous salmonids in the Pacific Northwest. *American Fisheries Society Symposium*, 17, 334–349.
- REICE, S.R., WISSMAR, R.C. AND NAIMAN, R.J., 1990. Disturbance regimes, resilience, and recovery of animal communities and habitats in lotic ecosystems. *Environmental Management*, 14, 647–659.
- REID, M.A. AND BROOKS, J.J., 2000. Detecting effects of environmental water allocations in wetlands of the Murray–Darling Basin, Australia. *Regulated Rivers: Research and Management*, 16, 479–496.
- REISER, D.W., RAMEY, M. P., BECK, S., LAMBERT, T.R. AND GEARY, R.E., 1989. Flushing flow recommendations for maintenance of salmonid spawning gravels in a steep regulated stream. *Regulated Rivers: Research and Management*, 3, 267–275.
- RESH, V.A., BROWN, A.V., COVICH, A.P., GURTZ, M.E., LI, H.W., MINSHALL, G.W., REICE, S.R., SHELDON, A.L., WALLACE, J.B. AND WISSMAR, R., 1988. The role of disturbance in stream ecology. *Journal of the North American Benthological Society*, 7, 433–455.
- RICHTER, B.D., BAUMGARTNER, J.V., POWELL, J. AND BRAUN, D.P., 1996. A method for assessing hydrologic alteration within ecosystems. *Conservation Biology*, 10, 1163–1174.
- RICHTER, B.D., BAUMGARTNER, J.V., WIGINGTON, R. AND BRAUN, D.P., 1997. How much water does a river need? *Freshwater Biology*, 37, 231–249.
- RICHTER, B.D., MATTHEWS, R., HARRISON, D.L. AND WIGINGTON, R., 2003. Ecologically sustainable water management: managing river flows for ecological integrity. *Ecological Applications*, 13, 206–224.
- RILEY, W.D., EAGLE, M.O., IVES, M.J., RYCROFT, P. AND WILKINSON, A., 2003. A portable passive integrated transponder multi-point decoder system for monitoring habitat use and behaviour of freshwater fish in small streams. *Fisheries Management and Ecology*, 10, 265–268.
- ROBERTS, J.H. AND ANGERMEIER, P.L., 2007. Spatiotemporal variability of stream habitat and movement of three species of fish. *Oecologia*, 151, 417–430.
- ROBINSON, C.T., TOCKNER, K. AND WARD, J.V., 2002. The fauna of dynamic riverine landscapes. *Freshwater Biology*, 47, 661–677.

- RODRIGUEZ, M.A. AND LEWIS, Jr., W.M., 1997. Structure of fish assemblages along environmental gradients in floodplain lakes of the Orinoco River. *Ecological Monographs*, 67, 109–128.
- RODRIGUEZ, M.A., 2002. Restricted movement in stream fish: the paradigm is incomplete, not lost. *Ecology*, 83, 1–13.
- ROGHAIR, C.N., DOLLOFF, C.A. AND UNDERWOOD, M.K., 2002. Response of a brook trout population and instream habitat to a catastrophic flood and debris flow. *Transactions of the American Fisheries Society*, 131, 718–730.
- ROSS, S.T. AND BAKER, J.A., 1983. The response of fishes to periodic spring floods in a Southeastern Stream. *American Midland Naturalist*, 109, 1–14.
- ROUSSEL, J.-M., HARO, A. AND CUNJAK, R.A., 2000. Field-test of a new method for tracking small fishes in shallow rivers using passive integrated transponder (PIT) technology. *Canadian Journal of Fisheries and Aquatic Sciences*, 57, 1326–1329.
- RUETZ, C.R. AND JENNINGS, C.A., 2000. Swimming performance of larval robust redbhorse *Moxostoma robustum* and low-velocity habitat modeling in the Oconee River, Georgia. *Transactions of the American Fisheries Society*, 129, 398–407.
- SABO, M.J. AND KELSO, W.E., 1991. Relationship between morphometry of excavated floodplain ponds along the Mississippi River and their use as fish nurseries. *Transactions of the American Fisheries Society*, 120, 552–561.
- SABO, M.J., KELSO, W.E., BRYAN, C.F. AND RUTHERFORD, D.A., 1991. Physicochemical factors affecting larval fish densities in Mississippi River floodplain ponds, Louisiana (U.S.A.). *Regulated Rivers: Research and Management*, 6, 109–116.
- SALO, J., 1990. External processes influencing origin and maintenance of inland water-land ecotones. In: NAIMAN, R.J. AND DECAMPS, H., eds. *The ecology and management of aquatic-terrestrial ecotones*. Paris: Unesco Publ., 37-64.
- SATO, T., 2006. Dramatic decline in population abundance of *Salvelinus leucomaenis* after a severe flood and debris flow in a high gradient stream. *Journal of Fish Biology*, 69, 1849–1854.
- SCHAEFER, J., 2001. Riffles as barriers to interpool movement by three cyprinids (*Notropis boops*, *Camptostoma anomalum* and *Cyprinella venusta*). *Freshwater Biology*, 46, 379–388.
- SCHEERER, P.D., 2002. Implications of floodplain isolation and connectivity on the conservation of an endangered minnow, Oregon chub, in the Willamette River, Oregon. *Transactions of the American Fisheries Society*, 131, 1070–1080.
- SCHIEMER, F. AND WAIDBACHER, H., 1992. Strategies for conservation of a Danubian fish fauna. In: BOON, P.J., CALOW, P. AND PETTS, G.E., eds. *River conservation and management*. Chichester, UK: Wiley, 363-382.
- SCHIEMER, F. AND ZALEWSKI, M., 1992. The importance of riparian ecotones for diversity and productivity of riverine fish communities. *Netherlands Journal of Zoology*, 42, 323–335.
- SCHIEMER, F., 2000. Fish as indicators for the assessment of the ecological integrity of large rivers. *Hydrobiologia*, 422/423, 271–278.
- SCHIEMER, F., BAUMGARTNER, C. AND TOCKNER, K., 1999. Restoration of floodplain rivers: the Danube restoration project. *Regulated Rivers: Research and Management*, 15, 231–244.
- SCHIEMER, F., GUTI, G., KECKEIS, H. AND STARAS, M., 2004. Ecological status and problems of the Danube River and its fish fauna: a review. In: WELCOMME, R. AND PETR, T., eds. *Proceedings of the second international symposium on the management of large rivers for fisheries: Volume I*. Bangkok, Thailand: FAO Regional Office for Asia and the Pacific, 273–299, (RAP Publication 2004/16).
- SCHIEMER, F., KECKEIS, H. AND KAMLER, E., 2003. The early life history stages of riverine fish: ecophysiological and environmental bottlenecks. *Comparative Biochemistry and Physiology (Part A)*, 133, 439–449.

- SCHIEMER, F., KECKEIS, H., RECKENDORFER, W. AND WINKLER, G. 2001a. The inshore retention concept and its significance for large rivers. *Archiv für Hydrobiologie Supplement*, 135, 509–16.
- SCHLOSSER, I.J., 1985. Flow regime, juvenile abundance and the assemblage structure of stream fishes. *Ecology*, 66, 1484–1490.
- SCHMIDT, J.C., WEBB, R.H., VALDEZ, R.A., MARZOLF, G.R. AND STEVENS, L.E., 1998. Science and values in river restoration in the Grand Canyon. *Bioscience*, 48, 735–747.
- SCHROEDER, K. AND SAVONEN, C., 1997. Lessons from floods. *Fisheries*, 22, 14–16.
- SCHULTZ, A.A., MAUGHAN, O.E. AND BONAR, S.A., 2003. Effects of flooding on abundance of native and nonnative fishes downstream from a small impoundment. *North American Journal of Fisheries Management*, 23, 503–511.
- SCHULZ, U. AND BERG, R., 1987. The migration of ultrasonically-tagged bream, *Abramis brama* (L.) in Lake Constance (Bodensee-Untersee). *Journal of Fish Biology*, 31, 409–414.
- SCHWARTZ, J.S. AND HERRICKS, E.E., 2005. Fish use of stage-specific fluvial habitats as refuge patches during a flood in a low-gradient Illinois stream. *Canadian Journal of Fisheries and Aquatic Sciences*, 62, 1540–1552.
- SEDELL, J.R., REEVES, G.H., HAUER, F.R., STANFORD, J.A. AND HAWKINS, C.P., 1990. Role of refugia in recovery from disturbances: modern fragmented and disconnected river systems. *Environmental Management*, 14, 711–724.
- SEDELL, J.R., RICHEY, J.E. AND SWANSON, F.J., 1989. The river continuum concept: A basis for the expected ecosystem behavior of very large rivers? *Canadian Special Publication of Fisheries and Aquatic Sciences*, 106, 49–55.
- SEEGRIST, D.W. AND GARD, R., 1972. Effects of floods on trout in Sagehen Creek, California. *Transactions of the American Fisheries Society*, 101, 478–482.
- SIMONS, J.H.E.J., BAKKER, C., SCHROPP, M.H.I., JANS, L.H., KOK, F.R. AND GRIFT, R.E., 2001. Man-made secondary channels along the River Rhine (The Netherlands); results of post-project monitoring. *Regulated Rivers: Research and Management*, 17, 473–491.
- SIMONSON, T.D. AND SWENSON, W.A., 1990. Critical stream velocities for young-of-year smallmouth bass in relation to habitat use. *Transactions of the American Fisheries Society*, 119, 902–909.
- SKALSKI, G.T. AND GILLIAM, J.F., 2000. Modelling diffusive spread in a heterogeneous population: a movement study with stream fish. *Ecology*, 81, 1685–1700.
- SKOV, C., BRODERSEN, J., BRONMARK, C., HANSONN, L.A., HERTONSSON, P. AND NILSSON, P.A., 2005. Evaluation of PIT-tagging in cyprinids. *Journal of Fish Biology*, 67, 1195–1201.
- SMITH, C., REICHARD, M., JURAJDA, P. AND PRZYBYLSKI, M., 2004. The reproductive ecology of the European bitterling (*Rhodeus sericeus*). *Journal of Zoology*, 262, 107–124.
- SMITHSON, E.B. AND JOHNSTON, C.E., 1999. Movement patterns of stream fishes in a Ouachita highlands stream: an examination of the restricted movement paradigm. *Transactions of the American Fisheries Society*, 128, 847–853.
- SNYDER, D.E., 2003. Invited review: conclusions from a review of electrofishing and its harmful effects on fish. *Reviews in Fish Biology and Fisheries*, 13, 445–453.
- SNYDER, E.B., EITEMILLER, D.J., ARANGO, C.P., UEBELACKER, M.L. AND STANFORD, J.A., 2003. Floodplain hydrologic connectivity and fisheries restoration in the Yakima River, U.S.A. *Verhandlungen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie*, 28, 1653–1657.
- SOMMER, T.C., HARRELL, W.C., KURTH, R., FEYRER, F., ZEUG, S.C. AND O'LEARY, G., 2004a. Ecological patterns of early life stages of fishes in a large river-floodplain of the San Francisco estuary. *American Fisheries Society Symposium*, 39, 111–123.

- SOMMER, T., BAXTER, R. AND HERBOLD, B., 1997. The resilience of splittail in the Sacramento–San Joaquin estuary. *Transactions of the American Fisheries Society*, 126, 961–976.
- SOMMER, T.R., CONRAD, L., O'LEARY, G., FEYRER, F. AND HARRELL, W.C., 2002. Spawning and rearing of splittail in a model floodplain wetland. *Transactions of the American Fisheries Society*, 131, 966–974.
- SOMMER, T.R., HARRELL, W.C. AND NOBRIGA, M.L., 2005. Habitat use and stranding risk of juvenile Chinook salmon on a seasonal floodplain. *North American Journal of Fisheries Management*, 25, 1493–1504.
- SOMMER, T.R., HARRELL, W.C., NOBRIGA, M., BROWN, R., MOYLE, P.B., KIMMERER, W.J. AND SCHEMEL, L., 2001a. California's Yolo Bypass: evidence that flood control can be compatible with fish, wetlands, wildlife and agriculture. *Fisheries*, 26, 6–16.
- SOMMER, T.R., HARRELL, W.C., SOLGER, A.M., TOM, B. AND KIMMERER, W., 2004b. Effects of flow variation on channel and floodplain biota and habitats of the Sacramento River, California, USA. *Aquatic Conservation-Marine and Freshwater Ecosystems*, 14, 247–261.
- SOMMER, T.R., NOBRIGA, M.L., HARRELL, W.C., BATHAM, W. AND KIMMERER, W.J., 2001b. Floodplain rearing of juvenile chinook salmon: evidence of enhanced growth and survival. *Canadian Journal of Fisheries and Aquatic Sciences*, 58, 325–333.
- SOUSA, W.P., 1984. The role of disturbance in stream natural communities. *Annual Review of Ecology and Systematics*, 15, 353–391.
- SPARKS, R.E., 1995. Need for ecosystem management of large rivers and floodplains. *Bioscience*, 45, 168–182.
- SPARKS, R.E., BAYLEY, P.B., KOHLER, S.L. AND OSBORNE, L.L., 1990. Disturbance and recovery of large floodplain rivers. *Environmental Management*, 14, 699–709.
- SPARKS, R.E., NELSON, J.C. AND YIN, Y., 1998. Naturalisation of the flood regime in regulated rivers. *Bioscience*, 48, 706–720.
- SPARREVOHN, C.R., NIELSEN, A. AND STØTTRUP, J.G., 2002. Diffusion of fish from a single release point. *Canadian Journal of Fisheries and Aquatic Sciences*, 59, 844–853.
- SPENCER, S.R., CAMERON, G.N. AND SWIHART, R.K., 1990. Operationally defining home range: temporal dependence exhibited by hispid cotton rats. *Ecology*, 71, 1817–1822.
- STAAS, S. AND NEUMANN, D., 1996. The occurrence of larval and juvenile 0+ fish in the Lower River Rhine. *Archiv für Hydrobiologie Supplement*, 113, 325–332.
- STANFORD, J.A., WARD, J.V., LISS, W.J., FRISSELL, C.A., WILLIAMS, R.N., LICHTATOWICH, J.A. AND COUTANT, C.C., 1996. A general protocol for restoration of regulated rivers. *Regulated Rivers: Research and Management*, 12, 391–413.
- STOTT, B., 1967. The movements and population densities of roach (*Rutilus rutilus* L.) and gudgeon (*Gobio gobio* L.) in the River Mole. *Journal of Animal Ecology*, 36, 407–423.
- SUAREZ, Y.R., PETRERE, M. Jr. AND CATELLA, A.C., 2001. Factors determining the structure of fish communities in Pantanal lagoons (MS, Brazil). *Fisheries Management and Ecology*, 8, 173–186.
- SUMMERFELT, R.C. AND MOSIER, D., 1984. Transintestinal expulsion of surgically implanted dummy transmitters by channel catfish. *Transactions of the American Fisheries Society*, 113, 760–766.
- SUMMERS, D.W., ROBERTS, D.E., GILES, N. AND STUBBING, D.N., 2006. Retention of visible implant and visible implant elastomer tags in brown trout in an English chalk stream. *Journal of Fish Biology*, 68, 622–627.
- SWALES, S., STOREY, A.W., RODERICK, I.D. AND FIGA, B.S., 1999. Fishes of floodplain habitats of the Fly River system, Papua New Guinea, and changes

- associated with El Niño droughts and algal blooms. *Environmental Biology of Fishes*, 54, 389–404.
- SWANBERG, T.R. AND GEIST, D.R., 1997. Effects of intraperitoneal transmitters on the social interaction of rainbow trout. *North American Journal of Fisheries Management*, 17, 178–181.
- SWANBERG, T.R., 1997. Movements and habitat use by fluvial bull trout in the Blackfoot river, Montana. *Transactions of the American Fisheries Society*, 126, 735–746.
- SWANSON, F.J., JOHNSON, S.L., GREGORY, S.V. AND ACKER, S.A., 1998. Flood disturbance in a forested mountain landscape. *Bioscience*, 48, 681–689.
- TEJERINA-GARRO, F.L., FORTIN, R. AND RODRIGUEZ, M., 1998. Fish community structure in relation to environmental variation in floodplain lakes of the Araguaia basin. *Environmental Biology of Fishes*, 51, 399–410.
- TEW, K.S., HAN, C.C., CHOU, W.R. AND FANG, L.S., 2002. Habitat and fish fauna structure in a subtropical mountain stream in Taiwan before and after a catastrophic typhoon. *Environmental Biology of Fishes*, 65, 457–462.
- THARME, R.E., 2003. A global perspective on environmental flow assessment: emerging trends in the development and application of environmental flow methodologies for rivers. *Rivers Research and Applications*, 19, 397–441.
- THEDINGA, J.F., MOLES, A. AND FUJIOKA, J.T., 1997. Mark retention and growth of jet-injected juvenile marine fish. *Fishery Bulletin*, 95, 629–633.
- THIEME, M.L., MCIVOR, C.C., BROUDER, M.J. AND HOFFNAGLE, L., 2001. Effects of pool formation and flash flooding on relative abundance of young-of-year flannelmouth suckers in the Paria River, Arizona. *Regulated Rivers: Research and Management*, 17, 145–156.
- THOMPSON, J. M., HIRETHOTA, P.S. AND EGGOLD, B.T., 2005. A comparison of elastomer marks and fin clips as marking techniques for walleye. *North American Journal of Fisheries Management*, 25, 308–315.
- THOMS, M.C., 2003. Floodplain-river ecosystems: lateral connections and the implications of human interference. *Geomorphology*, 56, 335–349.
- THOMS, M.C., SOUTHWELL, M. AND MCGINNESS, H.M., 2005. Floodplain-river ecosystems: Fragmentation and water resources development. *Geomorphology*, 71, 126–138.
- THORP, J.H. AND DELONG, M.D., 1994. The riverine productivity model: an heuristic view of carbon sources and organic processing in large river ecosystems. *Oikos*, 70, 305–308.
- TOCKNER, K. AND BRETSCJKO, G., 1996. Spatial distribution of particulate organic matter (POM) and benthic invertebrates in a river-floodplain transect (Danube, Austria): importance of hydrological connectivity. *Archiv für Hydrobiologie Supplement*, 115, 11–27.
- TOCKNER, K., AND STANFORD, J.A., 2002. Riverine flood plains: present state and future trends. *Environmental Conservation*, 29, 308–330.
- TOCKNER, K., BAUMGARTNER, C., SCHIEMER, F. AND WARD, J.V., 2000a. Biodiversity of a Danubian floodplain: structural, functional and compositional aspects. In: GOPAL, B., JUNK, W.J. AND DAVIS, J.A., eds. *Biodiversity in wetlands: assessment, function and conservation: Volume 1*. Leiden, the Netherlands: Backhuys Publishers, 141–159.
- TOCKNER, K., MALARD, F. AND WARD, J.V., 2000b. An extension of the flood pulse concept. *Hydrological Processes*, 14, 2861–2883.
- TOCKNER, K., SCHIEMER, F. AND WARD, J.V., 1998. Conservation by restoration: the management concept for a river floodplain system on the Danube River in Austria. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 8, 71–86.
- TOTH, L.A., ARRINGTON, D.A., BRADY, M.A. AND MUSZICK, D.A., 1995. Conceptual evaluation of factors potentially affecting restoration of habitat structure within the Channelized Kissimmee River ecosystem. *Restoration Ecology*, 3, 160–180.

- TOWNSEND, C.R., 1989. The patch dynamics concept of stream community ecology. *Journal of the North American Benthological Society*, 8, 36–50.
- TREXLER, J.C., 1995. Restoration of the Kissimmee River: a conceptual model of past and present fish communities and its consequences for evaluating restoration success. *Restoration Ecology*, 3, 195–210.
- TSCHAPLINSKI, P.J. AND HARTMAN, G.F., 1983. Winter distribution of juvenile coho salmon (*Oncorhynchus kisutch*) before and after logging in Carnation Creek, British Columbia, and some implications for overwinter survival. *Canadian Journal of Fisheries and Aquatic Sciences*, 40, 452–461.
- TURNER, T.F., TREXLER, J.C., MILLER, G.L. AND TOYER, K.E., 1994. Temporal and spatial dynamics of larval and juvenile fish abundance in a temperate floodplain river. *Copeia*, 1994, 174–183.
- TYUS, H.M., 1987. Distribution, reproduction, and habitat use of the razorback sucker in the Green River. *Transactions of the American Fisheries Society*, 116, 111–116.
- VALDEZ, R.A., HOFFNAGLE, T.L., MCIVOR, C.C., MCKINNEY, T. AND LEIBFRIED, W.C., 2001. Effects of a test flood on fishes of the Colorado River in Grand Canyon, Arizona. *Ecological Applications*, 11, 686–700.
- VAN DER NAT, D., TOCKNER, K., EDWARDS, P.J., WARD, J.V. AND GURNELL, A.M., 2003. Habitat change in braided floodplains (Tagliamento, NE-Italy). *Freshwater Biology*, 48, 1799–1812.
- VAN DIJK, G.M., MARTEIJN, E.C.L. AND SCHULTE-WÜLWER-LEIDIG, A., 1995. Ecological rehabilitation of the River Rhine: plans, progress and perspectives. *Regulated Rivers: Research and Management*, 11, 377–388.
- VAN DIJK, P.L.M., HARDEWIG, I. AND HÖLKER, F., 2005. Energy reserves during food deprivation and compensatory growth in juvenile roach (*Rutilus rutilus* L.): the influence of season and temperature. *Journal of Fish Biology*, 66, 167–181.
- VANNOTE, R.L., MINSHALL, G.W., CUMMINS, K.W., SEDELL, J.R. AND CUSHING, C.E., 1980. The river continuum concept. *Canadian Journal of Fisheries and Aquatic Sciences*, 37, 130–137.
- WAIDBACHER, H., HEPP, H., KOVACEK, H., LEUTGEB, H. AND ZAUNER, G. 1989. The influence of bank structuring on fish populations. In: HARY, N. AND NACHTNEBEL, H.P. eds. *Landscaping for the Altenworth backwater area – Ecosystem study Altenworth*. Österreichische Akademie der Wissenschaften, Veröffentlichungen des Österreichischen MaB-Programms, Band 14, Universitätsverlag Wagner, Innsbruck, 123–161. (In German, English summary.)
- WALKER, K.F., SHELDON, F. AND PUCKRIDGE, J.T., 1995. A perspective on dryland river ecosystems. *Regulated Rivers: Research and Management*, 11, 85–104.
- WALSH, M.G. AND WINKELMAN, D.L., 2004. Anchor and visible implant tag retention by hatchery rain trout stocked into an Ozark stream. *North American Journal of Fisheries Management*, 24, 1435–1439.
- WALSH, M.G., BJORGO, K.A. AND ISELY, J.J., 2000. Effects of implantation method and temperature on mortality and loss of simulated transmitters in hybrid striped bass. *Transactions of the American Fisheries Society*, 129, 539–544.
- WARD, D.L., SCHULTZ, A.A. AND MATSON, P.G., 2003. Differences in swimming ability and behavior in response to high water velocities among native and nonnative fishes. *Environmental Biology of Fishes*, 68, 87–92.
- WARD, J.V. AND STANFORD, J.A., 1983. The serial discontinuity concept of lotic ecosystems. In: FONTAINE, T.D. AND BARTELL, S.M. *Dynamics of lotic ecosystems*. Ann Arbor, MI: Ann Arbor Science Publishers, 29–42.
- WARD, J.V. AND STANFORD, J.A., 1995a. Ecological connectivity in alluvial river ecosystems and its disruption by flow regulation. *Regulated Rivers: Research and Management*, 11, 105–119.
- WARD, J.V. AND STANFORD, J.A., 1995b. The serial discontinuity concept: extending the model to floodplain rivers. *Regulated Rivers: Research and Management*, 10, 159–168.

- WARD, J.V. AND TOCKNER, K., 2001. Biodiversity: towards a unifying theme for river ecology. *Freshwater Biology*, 46, 807–819.
- WARD, J.V., 1997. An expansive perspective of riverine landscapes: pattern and process across scales. *GAIA*, 6, 52–60.
- WARD, J.V., 1998a. Riverine landscapes: biodiversity patterns, disturbance regimes and aquatic conservation. *Biological Conservation*, 83, 269–278.
- WARD, J.V., 1998b. A running water perspective of ecotones, boundaries, and connectivity. *Verhandlungen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie*, 26, 1165–1168.
- WARD, J.V., MALARD, F. AND TOCKNER, K., 2002a. Landscape ecology: a framework for integrating pattern and process in river corridors. *Landscape Ecology*, 17, 35–45.
- WARD, J.V., ROBINSON, C.T. AND TOCKNER, K., 2002b. Applicability of ecological theory to riverine ecosystems. *Verhandlungen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie*, 28, 443–450.
- WARD, J.V., TOCKNER, K. AND SCHIEMER, F., 1999. Biodiversity of floodplain river ecosystems: ecotones and connectivity. *Regulated Rivers: Research and Management*, 15, 125–139.
- WARD, J.V., TOCKNER, K., ARSCOTT, D.B. AND CLARETT, C., 2002c. Riverine landscape diversity. *Freshwater Biology*, 47, 517–539.
- WASHINGTON, H.G., 1984. Diversity, biotic and similarity indices: a review with special relevance to aquatic ecosystems. *Water Research*, 18, 653–694.
- WEBB, P.W., 1989. Station-holding by three species of benthic fishes. *Journal of Experimental Biology*, 145, 303–320.
- WEBB, P.W., GERSTNER, C.L. AND MINTON, S.T., 1996. Station-holding by the mottled sculpin, *Cottus bairdi* (teleostei: cottidae), and other fishes. *Copeia*, 1996, 488–493.
- WEBER, E.D. AND FAUSCH, K.D., 2003. Interactions between hatchery and wild salmonids in streams: differences in biology and evidence for competition. *Canadian Journal of Fisheries and Aquatic Sciences*, 60, 1018–1036.
- WELCOMME, R.L. AND HALLS, A., 2001. Some considerations of the effects of differences in flood patterns on fish populations. *Ecohydrology and Hydrobiology*, 1, 313–321.
- WELCOMME, R.L. AND HALLS, A., 2004. Dependence of tropical river fisheries on flow. In: WELCOMME, R. AND PETR, T., eds. *Proceedings of the second international symposium on the management of large rivers for fisheries: Volume II*. Bangkok, Thailand: FAO Regional Office for Asia and the Pacific, 267–283, (RAP Publication 2004/17).
- WELCOMME, R.L., 1979. *Fisheries ecology of floodplain rivers*. London: Longman.
- WELCOMME, R.L., 1985. *River fisheries*. F.A.O. Fisheries Technical Papers 262.
- WELCOMME, R.L., 1995. Relationships between fisheries and the integrity of river systems. *Regulated Rivers: Research and Management*, 11, 121–136.
- WELCOMME, R.L., 2001. The status of large river habitats. In: COWX, I.G., ed. *Rehabilitation of freshwater fisheries*. Oxford: Fishing News Books, Blackwell Science, 11–20.
- WELCOMME, R.L., WINEMILLER, K.O. AND COWX, I.G., 2006. Fish environmental guilds as a tool for assessment of ecological condition of rivers. *River Research and Applications*, 22, 377–396.
- WENG, Z., MOOKERJI, N. AND MAZUMDER, A., 2001. Nutrient-dependent recovery of Atlantic salmon streams from a catastrophic flood. *Canadian Journal of Fisheries and Aquatic Sciences*, 58, 1672–1682.
- WERNER, E.E., GILLIAM, J.F., HALL, D.J. AND MITTELBAACH, G.G., 1983. An experimental test of the effects of predation risk on habitat use in fish. *Ecology*, 64, 1540–1548.
- WHITE, J.L. AND HARVEY, B.C., 2001. Effects of an introduced piscivorous fish on native benthic fishes in a coastal river. *Freshwater Biology*, 46, 987–995.

- WHITE, P.S. AND PICKETT, S.T.A., 1985. Natural disturbance and patch dynamics: an introduction. In: PICKETT, S.T.A. AND WHITE, P.S., eds. *The ecology of natural disturbance and patch dynamics*. New York: Academic Press, 3–13.
- WHITTON, B.A. AND LUCAS, M.C., 1997. Biology of the Humber rivers. *The Science of the Total Environment*, 194/195, 247–262.
- WILLIAMS, W.P., 1965. The population density of four species of freshwater fish, roach (*Rutilus rutilus* (L.)), bleak (*Alburnus alburnus* (L.)), dace (*Leuciscus leuciscus* (L.)) and perch (*Perca fluviatilis* (L.)) in the River Thames at Reading. *Journal of Animal Ecology*, 34, 173–185.
- WILLIS, T.J. AND BABCOCK, R.C., 1998. Retention and in situ detectability of visible implant fluorescent elastomer (VIFE) tags in *Pagrus pagrus* (Sparidae). *New Zealand Journal of Marine and Freshwater Research*, 32, 247–254.
- WINEMILLER, K.O. AND JEPSEN, D.B., 1998. Effects of seasonality and fish movement on tropical river food webs. *Journal of Fish Biology*, 53, 267–296.
- WINEMILLER, K.O., 2004. Floodplain river food webs: generalizations and implications for fisheries management. In: WELCOMME, R. AND PETR, T., eds. *Proceedings of the second international symposium on the management of large rivers for fisheries: Volume II*. Bangkok, Thailand: FAO Regional Office for Asia and the Pacific, 285–309, (RAP Publication 2004/17).
- WINEMILLER, K.O., TARIM, S., SHORMANN, D. AND COTNER, J.B., 2000. Fish assemblage structure in relation to environmental variation among Brazos River oxbow lakes. *Transactions of the American Fisheries Society*, 129, 451–468.
- WINTER, J.D., 1996. Advances in underwater biotelemetry. In: MURPHY, B.R. AND WILLIS, D.W., eds. *Fisheries techniques*. 2nd ed. Bethesda, Maryland: American Fisheries Society, 555–590.
- WOOD, P.J. AND ARMITAGE, P.D., 1997. Biological effects of fine sediment in the lotic environment. *Environmental Management*, 21, 203–217.
- WOODS, C.M.C AND MARTIN-SMITH, K.M., 2004. Visible implant fluorescent elastomer tagging of the big-bellied seahorse, *Hippocampus abdominalis*. *Fisheries Research*, 66, 363–371.
- WOODS, C.M.C. AND JAMES, P.J., 2003. Evaluation of visible implant fluorescent elastomer (VIE) as a tagging technique for spiny lobsters (*Jasus edwardsii*). *Marine and Freshwater Research*, 54, 853–858.
- WYDOSKI, R.S. AND EMERY, L., 1983. Tagging and marking. In: NIELSEN, A. AND JOHNSON, D.L., eds. *Fisheries techniques*. Bethesda, Maryland: American Fisheries Society, 215–237.
- ZARET, T.M. AND RAND, A.S., 1971. Competition in tropical stream fishes: support for the competitive exclusion principle. *Ecology*, 52, 336–342.
- ZEUG, S.C., WINEMILLER, K.O. AND TARIM, S., 2005. Response of Brazos River oxbow fish assemblages to patterns of hydrologic connectivity and environmental variability. *Transactions of the American Fisheries Society*, 134, 1389–1399.
- ZOLLNER, P.A. AND LIMA, S.L., 2005. Behavioral tradeoffs when dispersing across a patchy landscape. *Oikos*, 108, 219–230.
- ZYDLEWSKI, G.B., HARO, A., WHALEN, K.G. AND MCCORMICK, S.D., 2001. Performance of stationary and portable passive transponder detection systems for monitoring of fish movements. *Journal of Fish Biology*, 58, 1471–1475.

List of abbreviations

ANOVA	Analysis of Variance
DIDSON	Dual-Frequency Identification Sonar
DRIFT	Downstream Response to Imposed Flow Transformations
ESDC	Extended Serial Discontinuity Concept
FPC	Flood Pulse Concept
GLM	Generalised Linear Model
LSD	Least Significance Difference
PIT	Passive integrated transponder
RCC	River Continuum Concept
RPM	Riverine Productivity Model
RVA	Range of Variability Approach
SGR	Specific Growth Rate
SL	Standard Length
SPSS	Statistical Package for Social Sciences
VHS	Viral Haemorrhagic Septicaemia
VIE	Visible implant polymer
WFD	Water Framework Directive

Glossary

Alluvial	depositing soil or sediment
Anthropogenic	caused by human activity
Backwater	area of slack water alongside the main channel and in the mouths of tributaries
Benthic	associated with the bed of the water-body
Cyprinid	fish belonging to the genus Cyprinidae (carp and minnow-like species)
Diel	Occurring on a daily cycle
Ecotone	a transition area between two adjacent ecosystems
Eurytopic	generalist fish species such as roach and bleak
Hydroseral	The succession between open water and fen/bog habitats
Lentic	of slow-moving water
Limnophilic	associated with stillwater conditions or habitats
Lotic	of fast-moving water
Macrophyte	aquatic plants that grow in or near water
Ontogenetic	associated with the process of developing from egg or embryonic stages through to adult
Paleopotamon	rarely connected to the main river by flood waters
Parapotamon	permanently connected to the main river
Percids	fish species belonging to the family Percidae (Perches)
Photoperiod	the length of day and night, with days longer in the summer and shorter in the winter
Phytolithophilous	Fish species that deposit their eggs on aquatic plants or gravel/cobbles.
Phytophilous	Fish species that deposit their eggs on aquatic plants
Plesiopotamal	Associated with water bodies that are connected to the main river during annual periods of elevated flow
Plesiopotamon	connected to the main river during annual periods of elevated flow
Rheophilic	fish species that prefer to live in fast-moving water, such as chub and dace
Riparian	Of river banks and margins
Salmonid	Fish species belonging to the family Salmonidae
Succession	The process of progressive spatial or temporal replacement of species adapted to one set of conditions by species adapted to alternative sets of conditions along an environmental gradient, for instance temperature or moisture
Tannins	plant-derived aromatic compounds
Telemetry	remote measurement and data reporting
Terrestrialisation	Processes leading to development of land habitat from aquatic habitat

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Published by:

Environment Agency
Rio House
Waterside Drive, Aztec West
Almondsbury, Bristol BS32 4UD
Tel: 0870 8506506
Email: enquiries@environment-agency.gov.uk
www.environment-agency.gov.uk

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